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ADELPHA EROTIA EROTIA FORM "LERNA" (NYMPHALIDAE): EXPLORING A CORNER OF THE PUZZLE

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ABSTRACT. The larvae and pupa of *Adelpha erotia erotia* "lerna" are described and figured, and it is concluded that the taxon belongs to the *A. mesentina* species-group. *Cecropia longipes* is reported as the larval food plant. Relationships among the six *A. mesentina* group species are explored.

Additional key words: life history, Panama, Bombacaceae, Cecropiaceae, Malvaceae, Urticaceae

INTRODUCTION

The immature stages of any group of Lepidoptera, and the affiliations among their larval food plants, can provide valuable insights into species identities and alliances, and they can prove especially valuable in helping untangle a perplexing group, such as the speciose Neotropical genus *Adelpha* Hübner.

Adelpha dorsal wing patterns are confusing, and that has led to numerous misidentifications in widely consulted works, and hence to increasing confusion. Thus, for more than a century, *Adelpha* defied attempts to sort out its more than 350 published taxa, though the best did try (Godman & Salvin 1879–1901, Fruhstorfer 1907, Forbes unpublished manuscript). But difficulties of identification are now largely behind us, thanks to the recent revision of *Adelpha* by Willmott (2003b), who has taken us a giant leap forward in our understanding of this bewildering group. After evaluating all available type material and all published names, Willmott concluded that *Adelpha* comprises 85 species and 209 taxa. His detailed descriptions and color photographs make it possible at last to identify virtually any specimen with near certainty.

The task remains, to devise a satisfying classification for the group, one that reflects natural relationships. A major obstacle to understanding relationships within *Adelpha* is that the dorsal wing patterns are deceptive; species of similar appearance are not necessarily closely related, and closely related species do not necessarily resemble each other.

There is substantial evidence that dorsal wing patterns are mimetic, perhaps through Müllerian mimicry based on difficulty of capture (Mallet & Singer 1987, Srygley 1994) or through Batesian mimicry (Aiello 1984, Prudic et al. 2002). Though ventral wing patterns do provide some reliable characters useful in species identification, they also are subject to some variation directly resulting from selection on the dorsal wing pattern (Willmott personal communication). Like many other limenitidine genera, *Adelpha* is extremely homogeneous morphologically, both in wing pattern and genitalia, thus providing few reliable characters for phylogenetic analysis. Character systems other than adult morphology thus are essential for achieving a better understanding of *Adelpha* evolution and extant species relationships. The time is ripe for a molecular study of *Adelpha*. As well, the immatures and food plants offer a wealth of taxonomic information, but detailed and reliable knowledge of them is available for only about 25% of known *Adelpha* species (Müller 1886, Moss 1933, Aiello 1984, 1991, Otero & Aiello 1996, Freitas et al. 2001, Willmott 2003b, & references therein). For that reason, it is important for all who posses new information on *Adelpha* biology, to publish it. Even a small bit of new information can provide a valuable clue to species relationships, or offer support for or against suspected ones, and thus also shed light on the reliability of other characters. Here, I present information about the larvae, pupa, and larval food plant of *Adelpha e. erotia* form "lerna" (Hewitson, 1847), in the Republic of Panama, and point out possible alliances within the *A. mesentina* group, to which it belongs.

MATERIALS AND METHODS

Thirteen individuals were collected, 11 as larvae (representing various stadia) and two as pupae, on the dates, at the localities (all in Panama), under the lot numbers, and by the collectors listed in the appendix. Of these 13 individuals, one was preserved as a larva, five died as larvae and were preserved, one was preserved as a pupa, and six were reared to adults. Preservations were made by bringing the larva or pupa to a boil in distilled water, then dropping it into 80% ethanol. Adults were frozen, then pinned and spread.

Reared individuals were housed in petri dishes until fourth or early fifth stadium, then transferred to small cages fashioned from petri dishes and window

screening, and placed in Ziploc® bags with folded, moistened paper towel strips to regulate humidity. Pupae were suspended in the same type of cages, by taping their support silk to the covers. All reared individuals were maintained in an air-conditioned lab. Behaviors were observed and recorded daily (with few exceptions), and shed head capsules and pupal exuviae were collected and mounted.

Lot numbers for reared individuals consist of the year plus a sequential number. When more than one individual was reared, an individual number (#) is appended. Thus "lot 2000-20 #2" refers to individual #2 of the 20th lot for the year 2000. These numbers appear on the labels of all reared specimens and their associated parts, and correspond to numbers on daily data forms maintained by Aiello at the Smithsonian Tropical Research Institute (STRI), Republic of Panama. All material relating to these rearings, including plant vouchers, is at STRI.

The first individual reared (lot 1996-24) was identified by Keith Willmott, from a photograph showing dorsal and ventral views of the adult (Fig. 1), and is alluded to on page 174 of his *Adelpha* revision (Willmott 2003b).

First instar setal terminology follows Stehr (1987).

FIG. 1, *Adelpha erotia erotia* "lerna" adult, dorsal (left), ventral (right), lot 1996-24.

Head chalazae positions—second instar on—do not correspond to first instar setal positions, thus, chalaza and scolus terminology (Fig. 2 top) was devised and developed by Aiello and Willmott over the course of previous publications (Aiello 1984, Willmott 2003b) and in correspondence between us during the writing of this paper.

Plant classification follows Stevens (2001 onwards). Note that Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae, and several other families are now combined as the Malvaceae, and that Cecropiaceae is included in the Urticaceae.

RESULTS

All 11 larvae were found on *Cecropia longipes* Pittier, 1917 (Urticaceae) (plant vouchers Aiello 1588, 1612), in Parque Natural Metropolitano (PNM), on the Pacific side of the isthmus. Though *C. peltata* L., 1759, is more common in PNM, no evidence of *Adelpha* was found on it, and one larva (lot 2000-11) to which *C. peltata* was offered, ate some, then produced liquid fecula and died the next day. On the Atlantic side of the isthmus, *C. insignis* Liebm., 1851, the only *Cecropia* accessible from the Fort Sherman canopy crane, yielded no *Adelpha*. Though *C. obtusifolia* Bertol., 1840, is present in PNM, and, *C. longipes*, *C. obtusifolia*, and *C. peltata* are found at Fort Sherman, they were outside the areas accessible from the canopy cranes, and thus could not be searched.

Egg. Not seen.

First Instar. Head brown, with setae set in beige or gray pinacula in positions MD1, P1, P2, L1, AF1, AF2, F1, C1, A1, S1, S2, S3, SS1, and SS2, and with 3 setae on each half of labrum. Body pale greenish brown, with beige pinacula and bands of tiny beige spots that resemble pinacula but lack setae.

Second Instar. Head brown, densely dappled with pale, broadly conical chalazae—each with a terminal seta—representing three size groups. The principal chalazae—largest and plumpest—are arranged in four series—7 posterior, 4 medial, 2 anterior, 1 parafrontal. Among these, m1 and a1 are the most prominent. The spaces among the principals are filled by a few medium-sized and many small chalazae. The longest setae are found on the smallest chalazae, located on the lower portion of the head. All plain setae—i.e., set in pinacula—are confined to the mouthparts. Body yellow ocher above, brown on the sides, with short, yellow ocher scoli and gray chalazae and pinacula.

Third Instar. Head upper fourth, dark brown, with ocher chalazae; lower three-fourths gray, with small salmon-colored chalazae and still smaller gray ones; principal chalazae arranged in four series—7 posterior, 4 medial, 3 anterior, 1 parafrontal (minute or absent); the bases of the largest lumpy due to minute chalazae. Body pale ocher to salmon-brown dorsally, and dark gray to dark brown laterally, those ground colors mostly obscured by densely set, gray pinacula and chalazae; scoli stubby, ocher to salmon-brown, arranged as sub-dorsal and supra-spiracular on T2, T3, and A2-A7, and as only sub-dorsal on A8 and A10; spiracles dark brown, almost black.

Fourth Instar. Head now pale, with brown pits and numerous tiny chalazae surrounding the principal chalazae—otherwise similar in form and arrangement to the third instar. Body like third instar, but with a more pronounced 2-toned appearance, i.e., the sides of the thorax much darker than the rest of the body.

Fifth Instar (Figs 2 top left, top middle, and bottom; and 4 bottom left). Head cream-color to pale beige, with flat-bottomed pits of the same color, numerous setae set in minute chalazae, brown-marked frons, and dark brown mandibles; chalazae white, with conspicuous black-tips, and arranged in four series: 7 posterior, 6 medial, 4 anterior (a1 and a3 larger than a2 and a4), and 1 parafrontal. Body with thorax yellow ocher, mottled with red dorsally, chestnut brown laterally; abdomen yellow ocher with red mottling dorsally, cream-color laterally; simple, widely spaced setae arranged as several rings per body segment; chalazae white, ranging from tiny to long; subdorsal scoli (dorsal of Stehr 1987) (on T2–A8) large (except tiny on A1), white, with several tiers of black-tipped, black-based branches; supraspiracular scoli (on T2–A7) similar to subdorsals, but tiny and 2 or 3 branched; subspiracular scoli pale, tiny, grading from sessile and forked on anterior segments, to subsessile and 3–4 branched on

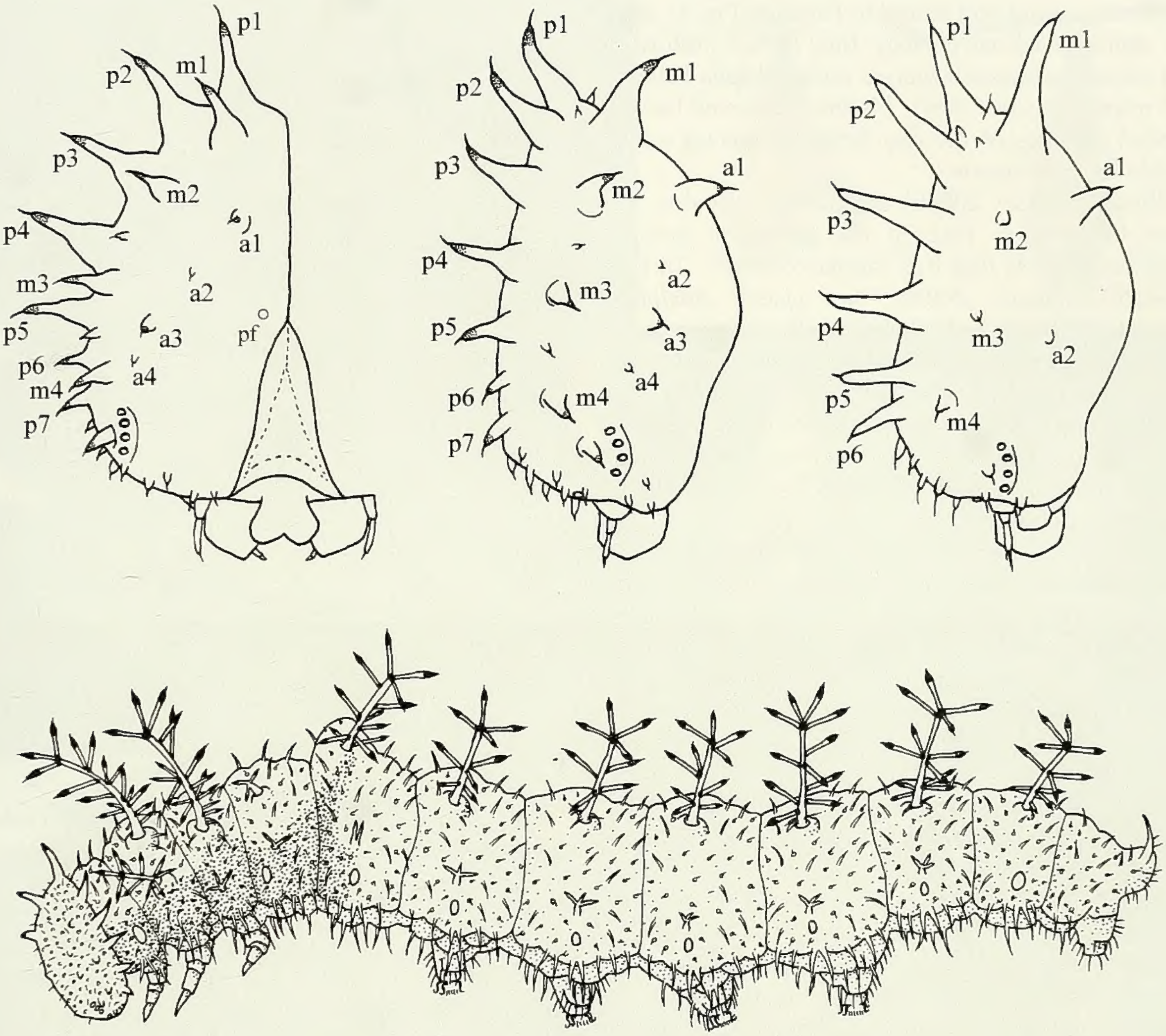

FIG. 2 Top, fifth instar head capsules: *Adelpha erotia erotia* "lerna" (lot 2000-29 #1) front view (left) and lateral view (middle); *Adelpha serpa celerio* (lot 1984-10 #2), lateral view (right); bottom, fifth instar habitus: *Adelpha e. erotia* "lerna," (lot 2000-29 #3). Chalazae: a = anterior, m = medial, p = posterior, pf = parafrontal.

posterior segments; caudal scolus simple, anteriorly curved; spiracles pinkish beige with dark brown borders.

A beautiful larva, whose white scoli with black tips and joints, and numerous white chalazae viewed against the yellow body give it a frosted appearance (Fig. 4 bottom left).

In mature larvae, abdominal segment 2 has a large, rounded, middorsal hump that corresponds to the huge A2 hook of the impending pupa.

Larval behavior. First instars constructed fecula and silk rods anchored to the leaf lobe margin, i.e., they were not leaf vein extensions, and rested head outward on them between feeding bouts and during molting. These rods were lengthened gradually, until they reached several times the body length of the larva. Second through fourth instars added tiny leaf bits to the base of their fecal rods, and continued to rest on them as before. First through third instar feeding damage was characterized by tiny holes all over the leaf, and fourth and fifth instars ate whole leaf. Following the molt to the final stadium, larvae abandoned their fecal rods entirely, and when disturbed assumed a head down, T1–A2 arched, A7–A10 up position.

Pupa (Fig. 3). Entirely dark bronzy brown except for an area of shimmering gold reflection on the dorsum of the thorax, from the inner curve of a T2 middorsal projection through the inner curve of a A2 middorsal hook. The A2 middorsal hook huge, fairly straight, with a wider, slightly curved apex, far surpassing the bluntly rounded tip of the T2 middorsal projection, and reaching almost to head level. Head "horns" small, rounded, very similar to, but narrower than those of *A. lycorias melanthe* (Bates, 1864). Pupation silk chestnut brown. Both field-collected pupae, were found suspended beneath leaves.

Development and eclosion times. See appendix.

POSITION WITHIN *ADELPHA*

The 2-toned, uniform-scoli larva and the "huge hook" pupa of *A. erotia erotia* "lerna" indicate that this taxon belongs to the *A. mesentina* group (Aiello 1984), which, so far comprises six species as outlined by Willmott (2003b, as *phylaca* group) [=group II of Aiello (1984, 1991)], and includes *A. mesentina* (Cramer, 1777), the

type species of the genus. The final instars of the four *A. mesentina* group taxa reared in Panama (Fig. 4) also share similar head morphology; they have 7 posterior and 4 anterior chalazae, whereas most *Adelpha* have 6 and 2 respectively (see Key). Neither preserved larvae nor head capsules of the two Brazilian species were available for examination.

Willmott (2003a, 2003b) tentatively includes *A. pollina* Fruhstorfer, 1915 in the *mesentina* group, though he suspects that it is misplaced there. In his revision (Willmott, 2003b) he places *Adelpha hesterbergi* Willmott & Hall, 1999 in the *A. capucinus* group, whereas in his cladograms (Willmott 2003a) it appears loosely allied with the *mesentina* group (as "*phylaca* group"), but is not commented on in the text. The immature stages and larval food plant(s) are unknown for either taxon, and their logical affiliations remain to be discovered.

Final stadium larvae of *A. e. erotia* "lerna" and *A. lycorias melanthe* share a number of characteristics not reported for other *Adelpha* species; both have a frosted appearance due to the contrasting dark tips and branch bases of their pale scoli and to the numerous tiny chalazae that further ornament the body; and in both, the A2 subdorsal scolus terminates in a whorl of subequal branches.

By contrast, final instar *A. phylaca pseudaethalia* Hall, 1938 and *A. messana messana* (C. & R. Felder, 1867) have uniformly brownish scoli and chalazae, set among plain setae; and one of the terminal branches of the A2 subdorsal scolus is elongate and upwardly inclined. They also share a dark, elliptical, lateral patch across the junction of abdominal segments 4 and 5, a feature not present in either *A. e. erotia* "lerna" or *A. lycorias melanthe*.

Moss (1933) does not comment on larval scolus form or color pattern in *A. mesentina* or *A. thesprotia* (C. & R. Felder, 1867), but does note that the two were "...so similar...in larva and pupa that no special observations were made." However, his illustrations are sufficiently clear to show that the larvae of those two species share the relatively unornamented body and dark contrasting elliptical spot with *A. phylaca pseudaethalia* and *A. m. messana*.

The pupa of *A. e. erotia* "lerna" is distinctive in having the A2 "hook" nearly straight, and surpassing the T2 projection, whereas in each of the other five *A. mesentina* group species (Fig. 4 shows the four Panamanian species) it is curved and directed towards the tip of the T2 projection, with which it forms a nearly closed circle. In *A. e. erotia* "lerna," the T2 projection is short and broadly rounded, whereas in the other five taxa it is drawn out to a rounded point.

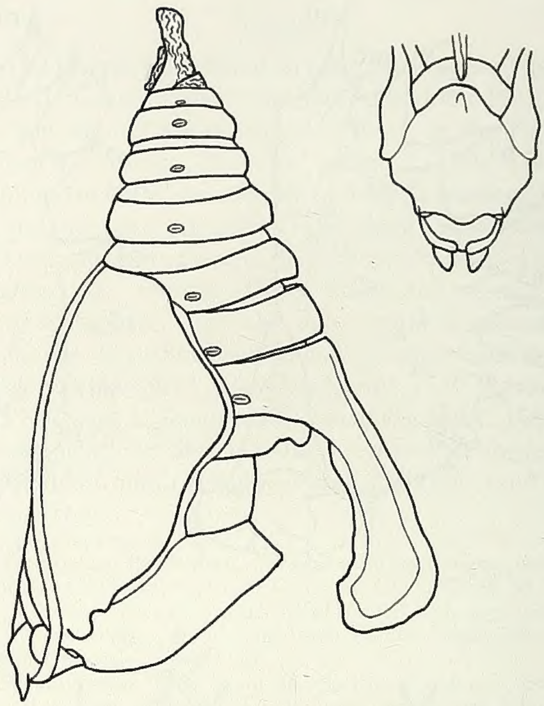

FIG. 3, *Adelpha erotia erotia* "lerna" pupa, lateral habitus and dorsal head and thorax (lot 1996-24).

Those unique features aside, the pupae of *A. e. erotia* "lerna" and *A. lycorias melanthe* resemble one another, and differ from *A. phylaca pseudaethalia* and *A. m. messana* in having the A2 "hook" apex slightly widened and truncate, instead of tapering to a rounded tip; and the "head horns" small and rounded, instead of outwardly curved points, or, as in *A. mesentina* and *A. thesprotia*, outwardly curved and leaf-like (Moss 1933). Though the illustrations in Moss (1933) are sufficiently detailed to comment on some characteristics of the latter two taxa, examination of preserved pupae or exuviae would be necessary to verify the form of the A2 "hook."

Combining published information on the group (Müller 1886, Moss 1933, Aiello 1984, 1991) and the present report, we now have descriptions of the larvae and pupae of at least one subspecies for each of the six, well-accepted members of the *A. mesentina* group. Based on those descriptions, *A. e. erotia* "lerna" and *A. lycorias melanthe* appear to form a subgroup, and the other four taxa another. Within the second subgroup, and based upon the form of the pupal "head horns," *A. phylaca pseudaethalia* appears to pair with *A. m. messana*, and *A. mesentina* with *A. thesprotia*.

The intra-group relationships suggested by the immature stages of the *mesentina* group are rather

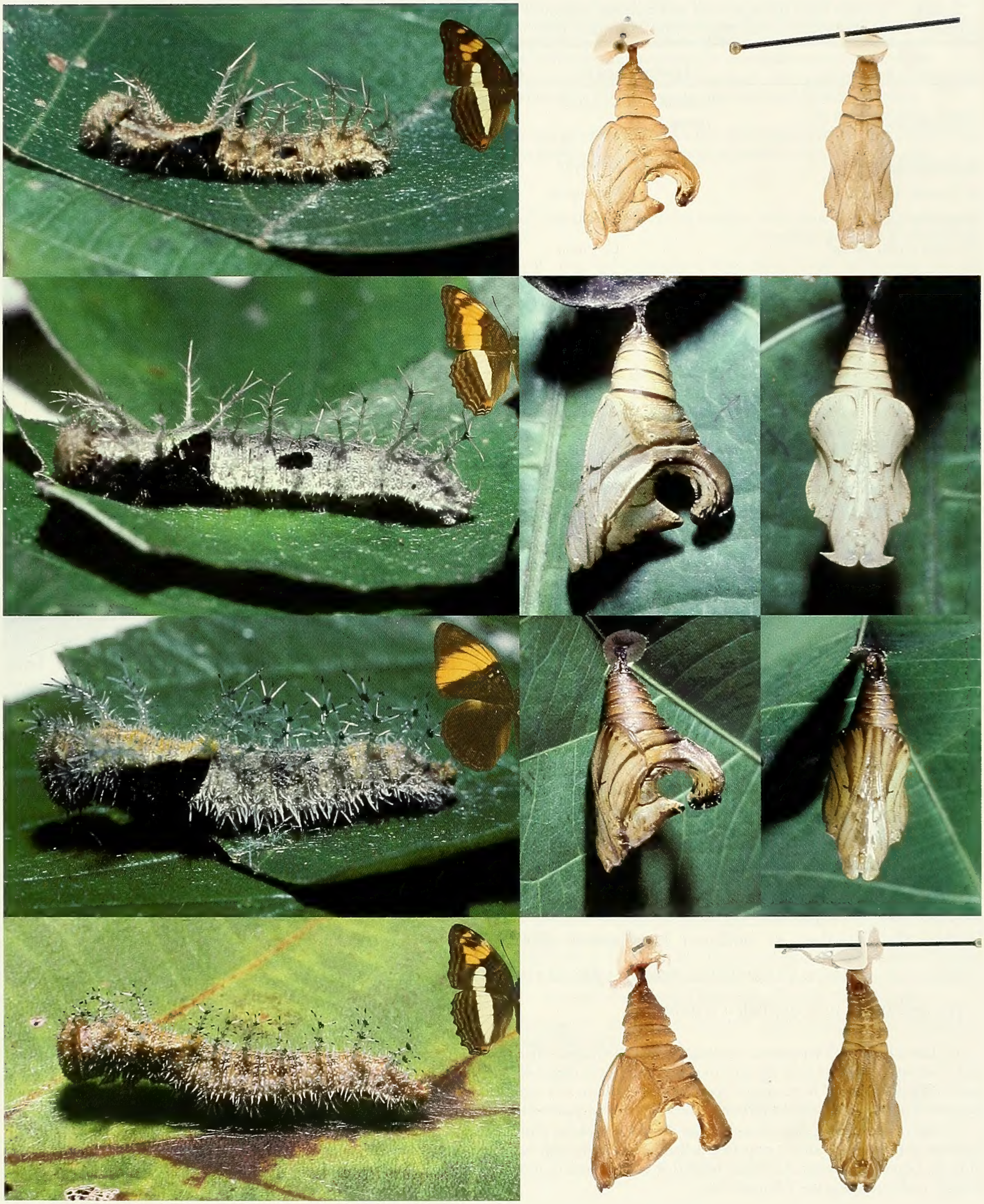

FIG. 4, Top row: *Adelpha messana messana* final instar, adult, pupal exuviae (lateral, ventral) (all lot 1989-22 #2); Second row: *A. phylaca pseudaethalia* final instar, adult, pupa (lateral, ventral) (all lot 1983-78); Third row: *A. lycorias melanthe* final instar, adult, pupa (lateral, ventral) (all 1983-8 #3); Bottom row: *A. e. erotia* "lerna" final instar and adult (lot 2000-20 #5), pupal exuviae (lateral, ventral) (lot 1996-24).

TABLE 1. Larval food plant genera and families reported for *Adelpha phylaca* Group taxa, for specimens with identifications verified. Plant classification follows Stevens (2001 onwards). Divisions reflect possible species affinities.

ADELPHA TAXON	ORDER ROSALES		ORDER MALVALES	REFERENCE
	Ulmaceae	Urticaceae	Malvaceae	
A. lycorias melanthe	*Trema*			Aiello 1984 (lot 83-8), as *melanthe*; Aiello lot 03-14
A. lycorias lycorias		*Cecropia*		Müller 1886, as *isis*
A. lycorias lycorias		*Coussapoa*		Müller 1886, as *isis*
A. lycorias lycorias		*Pourouma*		Müller 1886, as *isis*
A. erotia erotia "lerna"		*Cecropia*		Aiello lots 98-45, 00-20, 02-29
A. mesentina		*Pourouma*		Moss 1933
A. thesprotia		*Pourouma*	*Bombax*	Moss 1933, as *delphicola*
A. phylaca pseudaethalia		*Cecropia*		Aiello 1984 (lots 81-70, 82-39, 82-40, 83- 78), as *phylaca aethalia*; Aiello lot 00-27
A. messana messana			*Luehea*	Aiello 1990 (lot 89-22), as *ixia leucas*

different from those obtained by the cladistic analysis of Willmott (2003a), which relies strongly on adult characters. It is to be hoped that molecular studies will provide both a clearer concept of intra-group relationships and an assessment of the relative importance of immature and adult character sets.

LARVAL FOOD PLANTS OF THE *ADELPHA* MESENTINA GROUP

Though three plant families have been reported for members of the *A. mesentina* group (Table 1), the Urticaceae clearly dominate these records, and at least one member of each of the three *A. mesentina* group species-pairs has been reported on that plant family. The dominance of Urticaceae may prove greater once additional records (DeVries 1986, 1987; Janzen & Hallwachs 2004) of *A. lycorias melanthe* and *A. m. messana* on *Cecropia* are verified by Keith Willmott. Within the Rosales, as outlined by Stevens (2001 onward), Urticaceae (including *Cecropia*) and Ulmaceae, together with Cannabaceae and Moraceae, form a well-supported clade. Furthermore, within the Malvaceae, which comprise 9 subfamilies, the two that concern us here, Malvoideae and Bombacoideae, form their own well-supported clade. Thus, the *A. mesentina* group taxa are restricted to two small plant clades.

Two of the three plant families just discussed, have been reported as larval hosts in another *Adelpha* group, the *A. serpa* group: *A. celerio* on *Ochroma* (Malvaceae) (lot 1982-41) and *Cecropia* (Coley lot 15 in Aiello 1984); and an unidentified *Adelpha* taxon on *Heliocarpus* (Malvaceae) (lots 1982-75, 1983-68, 1985-122). Whether larval host plant switches and expansions have played an important role in *Adelpha* speciation cannot be determined until we have clearer knowledge of species relationships within *Adelpha*, and more complete information on host plant associations throughout the ranges of *Adelpha* taxa.

KEY TO PANAMANIAN *ADELPHA MESENTINA*-GROUP SPECIES BASED ON LARVAE AND PUPAE

p = posterior, m = medial, a = anterior

1a. Larva head with 6 posterior chalazae, 4 medial chalazae (in *serpa*-Group m1 is long and slender, and m2-m4 are low, rounded bumps), and 2 anterior chalazae (see fig. 2); frons bordered by a stripe of smooth relatively pit-less cuticle; body usually with A2 subdorsal scolus noticeably different in form and/or size from rest; thorax not significantly different in color or pattern from rest of body; pupa A2 dorsal projection not massive and not forming a circle with or surpassing the T2 dorsal projection **non-*mesentina* groups**

1b. Larva head with 7 posterior chalazae, 4 medial chalazae plus 2 or 3 tiny intercalated extras (sometimes not well aligned), and 4 anterior chalazae; pit-less stripe absent or poorly defined; main body scoli fairly uniform in shape and size; sides of thorax conspicuously darker than rest of body; pupa with a huge A2 dorsal hook that curves inward, nearly touching and forming a circle with the T2 dorsal projection, or nearly straight and surpassing the T2 projection **2**

2a. Larva head chalazae tipped with black or dark brown; body main scoli pale, with black or brown branch tips and bases; body also clothed with densely set, short, pale chalazae; all the above combine to give the larva a frosted appearance; head extra medial chalazae conspicuous and usually well aligned with principals, forming fairly uniform line; terminal branches of body A2 scolus similar to each other in length and inclination; abdomen without dark lateral patches; pupa head horns small and rounded. **3**

2b. Larva head and body scoli not dark-tipped, though larger branch junctions of main body scoli may be darkish; body also with short chalazae, but these not densely set, except perhaps laterally; head extra medial chalazae minute or small and often not well-aligned with principals; one terminal branch of body A2 subdorsal scolus noticeably longer than rest, and tilted upward; abdominal segment 5 with well-defined, dark brown lateral patch; pupa head horns outwardly curved, small, rounded or acute points, or outwardly curved and leaf-like. **4**

3a. Larva head chalazae slender conical, with somewhat rounded, conspicuously black tips; pits indistinct, same pale color as surrounding cuticle; pupa A2 dorsal hook nearly straight, and surpassing the T2 dorsal projection; T2 dorsal projection short and broadly rounded **_A. erotia erotia_ "lerna"**

3b. Larva head chalazae slender tapered, the larger ones with acute, dark tips; pits well-defined, a few darker than surrounding cuticle; pupa A2 dorsal hook curving inward to form nearly closed circle with T2 dorsal projection; T2 dorsal projection drawn out to a rounded point **_A. lycorias melanthe_**

4a. Pupa head horns outwardly curved, small, rounded or acute points **5**

4b. The larvae of *A. mesentina* and *A. thesprotia* have not been examined, but if they key to this couplet, then pupa head horns outwardly curved and leaf-like separates them from the two species keyed in couplet 5 **_A. mesentina_ and _A. thesprotia_**

5a. Larva head with 3 extra medial chalazae nearly same size as principals, one each between m1/m2, m2/m3, and m3/m4, but not well aligned with them, resulting in a ragged line; pupa head horns very small, outwardly curved, rounded points **_A. messana messana_**

5b. Larva head with 2 tiny, extra medial chalazae, one each between m2/m3 and m3/m4, usually well aligned with principals; pupa head horns outwardly curved, pointed and leaf-like **_A. phylaca pseudaethalia_**

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Appendix: *Adelpha erotia erotia* "lerna" collection and developmental data (number of days in each stadium) and outcomes. Numbers include days spent preparing for molting or pupation, i.e., not eating. Final date is the date of eclosion, death, or preservation, and is not included in durations. Minimum durations (≥) are given for the stages collected or for stages cut short by preservation or natural death. A ≈ indicates a molt that may have occurred on a day when observations were not made.

Name and collection data	Lot#	Indiv#	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Pupa	Final date	Outcome
Collected as a pupa, suspended from leaf of *Mangifera indica*, near a *Cecropia* tree: **Coclé Province**, El Copé, 200 meters above El Harino school, on the road to la cruz del misionero ("calvario"), by Annette Aiello and Ricardo Cortez										
20 Nov. 1996	1996-24	1						≥14	4 Dec	**Adult** ♂, eclosion: c.0930 hours
Collected as a pupa, suspended from a leaf of *Cecropia longipes*: **Panama Province**, Parque Natural Metropolitano canopy crane, by Joe Wright and Mirna Samaniego										
17 Aug. 1998	1998-45	1						≥8	25 Aug	**Adult** ♀, eclosion: c.1200 hours
Collected as a third instar, eating *Cecropia longipes*: **Panama Province**, Parque Natural Metropolitano canopy crane, by Sunshine Van Bael										
9 Aug. 2000	2000-11	1			≥9	6	≥5	—	29 Aug	Larva died, preserved
Collected as early instars, eating *Cecropia longipes*: **Panama Province**, Parque Natural Metropolitano canopy crane, by Sunshine Van Bael										
6 Sep. 2000	2000-20	1	≥3	≈7	≈5	6	13	—	10 Oct	Larva (prepupa) died, preserved
13 Sep. 2000	2000-20	2	≥3	≈4	5	6	10	10	22 Oct	**Adult** ♀, eclosion: c.1000 hours
13 Sep. 2000	2000-20	3		≥6	≥2	—	—	—	21 Sep	Larva died, preserved
13 Sep. 2000	2000-20	4	2	≈3	≈6	8	10	10	23 Oct	**Adult** ♀, eclosion: c.1000 hours
13 Sep. 2000	2000-20	5	≥1	≈4	5	7	10	10	21 Oct	**Adult** ♀, eclosion time not obs.
20 Sep. 2000	2000-20	6		≥1	4	7	≥3	—	5 Oct	Larva died, preserved
27 Sep. 2000	2000-20	7			≥4	7	—	—	8 Oct	Larva died molting, preserved
Collected as early instars, eating *Cecropia longipes*: **Panama Province**, Parque Natural Metropolitano canopy crane, by Sunshine Van Bael										
24 Nov. 2000	2000-29	1				≥1	8	11	14 Dec	**Adult** ♂, eclosion: c.1030 hours
24 Nov. 2000	2000-29	2		≥4	3	7	8	≥2	18 Dec	Pupa ♂ preserved
24 Nov. 2000	2000-29	3		≥6	4	6	≥7	—	17 Dec	Larva preserved

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LARVAL HOST PLANT RECORDS OF ASTERACEAE ROOT-FEEDING EUCOSMINI IN CALIFORNIA AND ADJACENT STATES (TORTRICIDAE)

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ABSTRACT. We surveyed woody Asteraceae for root-boring lepidopteran larvae in California, Nevada, and Arizona. Data are reported for 21 species of the genera *Phaneta, Eucosma, Pelochrista, Epiblema,* and *Sonia* (Tortricidae: Eucosmini) reared from 23 species (14 genera) of Asteraceae. Among 80 rearing records, about half of the tortricids were recorded at multiple localities. One widespread species, *Eucosma ridingsana*, fed on several genera of Asteraceae at different localities, and *Sonia vovana* fed on species of two plant genera, whereas other species that we reared more than once were host specific to one or two plants of one genus. Larvae of seven other moth species were associated in these collections, probably as scavengers (Acrolophidae, Oecophoridae, Gelechiidae, macrothecine and phycitine Pyralidae, and Noctuidae). Literature reports of larval hosts for the tortricids are summarized

Additional key words: Lepidoptera, *Phaneta, Eucosma, Pelochrista, Epiblema, Sonia,* Arizona, Nevada, root-borer specificity, Acrolophidae, Oecophoridae, Gelechiidae, Pyralidae, Noctuidae.

INTRODUCTION

The Holarctic genera *Phaneta* and *Eucosma*, *Pelochrista*, and *Epiblema*, along with *Sonia* in the Nearctic, comprise an extremely species-rich group for which no phylogenetic classification has been proposed. Heinrich (1923) based the current classification of Nearctic species on presence/absence of a costal fold in the male, wing venation, and male genitalia. The Eucosmini, including this group of genera, warrants comprehensive study, including assessment of the female genital characters, which Heinrich omitted. There are more than 300 species of these five genera regarded as valid in America north of Mexico, about 60% of them in the western states, and many other species in collections remain unnamed.

Almost all species of the above named genera are endophagous, borers in stems, roots, or conifer cones, and those treated here comprise a guild feeding in roots of Asteraceae. Probably nearly all are specialists in larval host selection, but we lack host plant data for most and have only one record for many of those that have been reared. In 1966–68, as part of broader investigations on microlepidoptera biologies funded by the National Science Foundation, we conducted an extensive survey of tortricid borers in woody Asteraceae. Our study is the primary source of host data for western members of this guild. We present the data here, along with a few records from earlier and later years, in order to make them available for citing host plants in a book in progress on western moths and perhaps to lure researchers into further effort to rearing root-feeding caterpillars.

METHODS

We selected potential field sites for investigation based on past collections of adults, some of which were netted in association with particular composite shrubs, providing clues to their larval hosts. We visited identified localities about four weeks prior to recorded flight dates and searched for likely habitats, especially those dominated by *Chrysothamnus*, *Gutierrezia*, or "*Haplopappus*" (species of the last are now in *Ericameria*, *Hazardia*, *Isocoma*). Armed with narrow blade trenching spades, we dug up suspect shrubs and split open the root crowns to expose evidence of larval borers, exudations of sawdust-like frass. If a healthy colony of Eucosmini was present, we usually detected evidence within the first few plants; if not we spent an hour or more digging to locate a few potential larval galleries or become convinced none was present. When frass was detected, we clipped off lower roots and the above ground stems of the plant and placed the root crowns in plastic bags (45 × 20 cm) for transport in camp coolers. In the insectary, collections were housed in plastic bags lined with paper toweling, and each was reversed and aired out frequently in order to discourage fungal growth yet maintain sufficient moisture to avoid desiccation of larvae or pupae. Larvae were left in situ, and those that successfully transformed constructed emergence trackways leading to frass-encrusted silken turrets where the active pupae wedged enabling eclosion of the adults. When emergences began, the collections were checked daily to harvest newly emerged adult specimens. When moths failed to emerge from the pupal shell following metamorphosis,

identifications were made by genitalia dissections.

All collections were made by one or both of us, often accompanied by one or more student assistants (see acknowledgments). The rearing lot numbers were date-based, e.g. 68G23 = 1968, July, 23rd collection (except "I" was not used, so J-M = September to December). The number for each lot was assigned to notes on larval habits, moths and parasitoid specimens reared, and larvae preserved.

This information is summarized in an Access database. Voucher specimens are deposited in the Essig Museum of Entomology, University of California, Berkeley.

Plant nomenclature and authorship has been updated from that used on our specimen labels and follows The Jepson Manual (Hickman 1993).

Abbreviations: **II** to **XII** = February to December; **emgd.** = dates adults emerged; **n** = number of individuals reared; **AZ** = Arizona. **CA** = California, **NV** = Nevada; **Co.** = County; **Mts.** = Mountains; **Cr.** = Creek; **Vy.** = Valley; **campgr.** = campground; **mi.** = miles; **N, E, S, W, NE** etc. = compass directions

RESULTS

Our efforts produced about 80 rearing records of root-boring Eucosmini from approximately 135 Asteraceae collections processed, including one or more species from 66 collections, 2 or more from 11 collections. In total, we reared 21 species of *Phaneta*, *Eucosma*, *Pelochrista*, *Epiblema*, and *Sonia* from 23 species (14 genera) of Asteraceae, about half of the tortricids from multiple localities. We found one widespread species, *Eucosma ridingsana*, feeding on several genera of Asteraceae at different localities, and *Sonia vovana* fed on both *Gutierrezia* and *Isocoma*; whereas other species for which we had multiple records were host specific to one or two congeneric plants. A species of *Eucosma* and a *Phaneta* or *Sonia* sometimes occupied the same roots, but two congeneric species did so only once, when a single *E. canariana* was reared along with several *E. crambitana*.

Confined females of *Eucosma sandiego* laid large numbers of eggs in crevices and irregularities on the surface of bark and dirt clods, as well as on container sides. Evidently oviposition normally occurs on bark near the base of the plant, and young larvae burrow downward in above ground stems and into the root crowns in later instars. Larvae usually do not penetrate the deeper roots of smaller diameter, but in smaller plants such as *Gutierrezia*, larvae feed on slender roots by scoring a groove and covering the open side with silk and debris. Late instar larvae were found oriented either head upward or downward but eventually form a pupal cell head upward. Emergence is via a track leading to a frass-covered turret at or above ground level. We did not detect a diapause in any of the species we reared.

The roots often are shared by larvae of beetles, especially Cerambycidae and Curculionidae, and by various other insects that invade secondarily. Along with the Eucosmini, we list associated species of Lepidoptera of several families that were reared, all of which probably are detritivores.

Species accounts

Phaneta offectalis (Hulst, 1886)

Senecio spartioides.—68G14: CA, Mono Co., Crooked Creek, White Mts., 10,000', VII.10.1968 (n = 3, emgd. VIII.21/30).

Heinrich (1923) recorded "*Artemisia*" as a food plant of *offectalis*, whereas Sites and Phillip (1989) reared it from *Senecio riddelli*. MacKay (1959) described the larva based on specimens labeled "loco-weed" [*Astragalus* or *Oxytropis*?, Fabaceae], a 1947 collection of larvae from College Station, Texas. This may have been a misidentification of the plant.

Phaneta bucephaloides (Walsingham, 1891)

Chrysothamnus nauseosus. — 68G23: CA, Mono Co., 3 mi. S Lee Vining, VII.11.1968 (n = 3 emgd. VII.29). 68G28: CA, same locality, VII.19.1968 (n = 2, emgd. VIII.5). 68G66: CA, Lassen Co., 3 mi. S Litchfield, VII.24.1968 (n = 19, emgd. VIII.23 to IX.9).

Chrysothamnus viscidifolius.— 68G37: NV, Nye Co., Currant Creek campgr. VII.21.1968 (n= 1, emgd. VIII.21). 68G51: CA, Modoc Co., 8 mi. S Eagleville, VII.23.1968 (n = 1, dead ex pupal shell).

Associated species: 68G23, 68G37 *Eucosma crambitana*; 68G37 *E. canariana*; 68G66 *Alpheias* sp. (Pyralidae).

Engelhardt reared *bucephaloides* from *Chrysothamnus linifolius* in western Colorado (Heinrich 1929) and MacKay (1959) described the larva from the same collection.

Phaneta sp. near ***bucephaloides***

Chrysothamnus viscidifolius: 68G8: CA, Mono Co., Mono Lake, VII.9.1968 (n =1, emgd. IX.9). 68G13: CA, Inyo Co., Westgard Pass, VII.10.1968 (n =1, emgd. VIII.8). 68G35: NV, Nye Co., Currant Cr. campgr. VII.20.1968 (n =1, emgd. IX.9). 68G39: NV, Eureka Co., 3 mi. SE Eureka, VII.21.1968 (n = 1, dead in pupal shell).

Associated species: 68G35 *Alpheias* sp. (Pyralidae),

Eucosma crambitana (Walsingham, 1879)

Chrysothamnus nauseosus.— 68G15: CA, Inyo Co., 5 mi. N Big Pine, VII.10.1968 (n = 1, emgd. IX.5). 68G23: CA, Mono Co., 3 mi. S Lee Vining, VII.11.1968 (n = 13, emgd. VIII.16 to IX.11). 68G28: same locality, VII.19.1968 (n = 3, emgd. VIII.23 to IX.16). 68G48: NV, Washoe Co., 26 mi. N Gerlach, VII.23.1968 (n = 1, dead in pupal shell). 68G66: CA, Lassen Co., 3 mi. S Litchfield, VII.24.1968 (n = 19, emgd. VIII.23 to IX.9).

Chrysothamnus viscidiflorus.—68G3, G4: CA, Mono Co., Topaz Lake, VII.8.1968 (n = 3; emgd. VIII.23/26). 68G37: NV, Nye Co., Currant Creek campgr. VII.21.1968 (n = 4, emgd. VIII.26).

Associated species: 68G23, 68G37 *Phaneta bucephaloides*; 68G37 *E. canariana*; 68G66 *Alpheias* sp. (Pyralidae).

Eucosma sp. near **crambitana**

Ericameria ericoides. - 66J34: CA, Monterey Co., Seaside, IX.27.1966 (n = 1, emgd. X.3).

Ericameria linearifolia. - 67K93: CA, San Luis Obispo Co., Upper Cuyama Vy., X.6.1967 (n = 5, emgd. X.9/23). 68J20: CA, Ventura Co., Cuyama Vy., 2.8 mi. N Ozena jct., IX-11-1968 (n = 1, emgd. IX.19).

Eucosma canariana Kearfott, 1907

Chrysothamnus viscidiflorus. —68G37: NV, Nye Co., Currant Creek campgr. VII.21.1968 (n =1 emgd. VIII.5).

Associated species: *E. crambitana*, *Phaneta bucephaloides*; *Alpheias* sp. (Pyralidae).

Eucosma aurilineana Ferris, 2005

Chrysothamnus viscidiflorus. —68G11: CA, Mono Co., Toms Place, VII.9.1968 (n = 1, emgd. VIII.28).

Eucosma ridingsana (Robinson, 1869)

Grindelia hirsutula. —66J25: CA, Contra Costa Co., Pt. Molate beach, IX.21.1966 (n = 4, emgd. IX.22 to X.3).

Lessingia filaginifolia.—67D39: CA, San Luis Obispo Co., Oso Flaco dunes, IV.12.1967 (n = 1, emgd. by X.12). 68D194: same locality, IV.27.1968 (n = 2, emgd. VII.22,24).

Gutierrezia microcephala.—64H2: CA, San Diego Co., Boulevard, VIII.9.1964 (n = 1, emgd. IX.24). 68F60: CA, San Diego Co., 1 mi E. Jacumba, VI.7.1968 (n = 1, emgd. dead by IX).

Gutierrezia sp.—68F18: AZ, Mohave Co., NE of Kingman, VI.3.1968 (n = 2, emgd. VIII.19). 68F33: AZ, Yavapai Co., 7 mi. NE Bridgeport, VI.4.1968 (n = 4, emgd. VIII.12/26). 68F34: AZ, Yavapai Co., 15 mi. NE Prescott, VI.4.1968 (n = 1, emgd, VIII.19). 68F41: AZ, Gila Co., 1 mi. S Rye, VI.5.1968 (n = 3, emgd. VIII.22 to IX.5).

Isocoma menziesii.—68H28: CA, San Diego Co., Mission Dam, VIII.26.1968 (n = 1, emgd. X.1).

E. ridingsana was reared by Clarke from *Heterotheca villosa* in southeastern Washington (Brown *et al*.1983) and from *Gutierrezia* by Hetz and Werner (1969) in Arizona. Heinrich (1923) gave a questioned record, root-borer in "greasewood ?(*Sarcobatus vermiculatus*?)" (Chenopodiaceae), which was repeated by MacKay (1959), based on a 1915 collection of larvae from El Paso Co, Colorado. The records by Prentice (1965) as a shoot borer in *Pinus ponderosa* and *P. contorta* in British Columbia are erroneous, and possibly refer to *E. sonomana* Kearfott.

Associated species: 68H28 *Battaristis pasadenae* (Keifer) (Gelechiidae); 68F11 *Tathorhynchus exsiccatus* (Lederer) (Noctuidae).

Eucosma caniceps (Walsingham, 1884)

Artemisia tridentata.—68G1: CA, Mono Co., Leavitt Meadows, VII.8.1968 (n = 2, emgd. VII.22,25).

Artemisia (shrub, not *tridentata* ?).—68G19: CA, Inyo Co., 6 mi. S Bishop, VII.11.1968 (n = 5; emgd. VIII.26 to IX.24).

Eucosma avalona McDunnough, 1938

Artemisia californica.—67D42: CA, Santa Barbara Co., Cuyama River, 11 mi. ENE Santa Maria, IV.27.1967 (n = 2, emgd. by X).

Eucosma sandiego Kearfott, 1908

Isocoma acradenia.—67K1: CA, Kern Co., W of Caliente, X.1.1967 (n = 1, dead in pupal shell).

Isocoma menziesii.—all CA, San Diego Co.: 66J10: 4 mi SE El Cajon, IX.2.1966 (n = 1, emgd. X.28). 66J13: (pale desert race) Scissors Crossing, IX.2.1966 (n = 26, emgd. IX.6/29). 67K59: 4 mi SE El Cajon, X.4.1967 (n = 25, emgd. X.8/17). 67K79: Cardiff-by-the-Sea, X.6.1967; n = 4, emgd. X.11).

Associated species: 66J13, 67K79 *Amydria obliquella* Dietz (Acrolophidae); 66J10, 67K59 *Battaristis pasadenae* Keifer (Gelechiidae); 66J10 *Isophrictis* sp. (Gelechiidae); 66J10, 67K59, K79 *Sonia filiana*.

Eucosma optimana Dyar, 1893

Artemisia tridentata.—all CA, Mono Co.: 68G2: Topaz Lake, VII .8.1968 (n = 1, emgd. dead IX). 68G5:1 mi. NE Walker, VII .8.1968 (n = 2; emgd. IX.9/20). 68G7: Mono Lake, VII.9.68 (n = 1, emgd. VIII.26).

Eucosma laticurva Heinrich, 1929

Erigeron inornatus.—68G69: CA, Plumas Co., SW

edge Plumas-Eureka State Park, VII.27.1968 (n = 2, emgd. VIII.5, IX.25).

Eucosma maculatana (Walsingham, 1879)

Eriophyllum lanatum.—67D143: CA, Marin Co., 6 mi. SE Nicasio, IV.30.1967 (n = 2, emgd. VI.2). 68D177: CA, San Benito Co., Limekiln Canyon, IV.24.1968 (n = 2, emgd. V.30).

Eucosma williamsi Powell, 1963

Baccharis pilularis.—67D34.1: CA, San Luis Obispo Co., 5 mi. N Creston, IV.11.1967 (n = 1, emgd. VI.3). 67D43: CA, Santa Barbara Co., Cuyama River,11 mi. ENE Santa Maria, IV.12.1967 (n = 30, emgd, V.27 to VI.29).

The original series of this species was reared by F. X. Williams from larvae boring in roots of *B. pilularis* in February in the Oakland Hills, Alameda Co., CA, adults emerging in July (Powell 1963). De Benedictis *et al.* (1990) also reared this species at San Bruno Mt., San Mateo Co., from the same plant.

Pelochrista metariana (Heinrich, 1923), species complex

Heliomeris multiflora.—68G32: NV, Esmeralda Co., Lida Summit, VII.20.1968 (n = 14, emgd. VIII.5/19).

Pelochrista passerana (Walsingham, 1879)

Achillea millefolium.—04B38: CA, Santa Barbara Co., Santa Barbara Island, II.23. 2004 (n = 3, emgd. VI.1,2).

Epiblema strenuana (Walker, 1863) (beach form, differs phenotypically from typical *strenuana*)

Ambrosia chamissonis.—78J3: CA: Santa Barbara Co., Prisoners Harbor, Santa Cruz Id., IX.25.1978 (n = 1 emgd. X.29). 88M3: CA: Contra Costa Co., Point Molate beach, XII.12.1988 (n = 8, emgd. I.10 to II.19.1989). 92F15: CA: Contra Costa Co., Richmond Field Station, VI.24.1992 (n = 6, emgd. VII.5/19). 95D100: CA: Santa Barbara Co., Cluster Point, Santa Rosa Id., IV.29.1995 (n = 2, emgd. VI.12).

The larvae bore in the woody stems, which act as rhizomes for the spreading plant, at or just beneath the sand surface. Presence of larvae is evidenced by accumulations of frass at nodes or breaks in the brittle stems. On *A. psilostachya* at Antioch dunes Natl. Wildlife Refuge, Contra Costa Co., growing on riverine sand dunes, larvae of *strenuana* burrowed into vegetative terminals and downward in the above ground stems.(82E92, 82F13, 91H23). Typical populations of *E. strenuana* have been reared from Asteraceae in the subtribe Ambrosiinae, including other *Ambrosia* species, *Parthenium*, and *Xanthium*, in widespread parts of North America, recorded by Heinrich (1923), MacKay (1959), Miller and Pogue (1984) and others.

Sonia vovana (Kearfott, 1907)

Gutierrezia californica.—64H2: CA, San Diego Co., Boulevard, VIII.9.1964 (n = 1, emgd. by IX.25). 66H13: CA, Kern Co., McKittrick, VIII.30.1966 (n = 3, emgd. IX.12/ 22). 68H24: CA, Riverside Co., La Sierra College, VIII.22.1968 (n = 5, emgd. IX.13 to X.1).

Gutierrezia microcephala [= *lucida* ?]. - 66H20: CA, Los Angeles Co., 2 mi. S Lancaster, VIII.31.1966 (n =1, emgd. IX.5). 66J2: CA: San Bernardino Co., 2 mi. SE Desert Springs [now Pinon Hills], IX.1.1966 (n = 1, emgd. IX.7). 66J16: CA, Los Angeles Co., 2 mi. N. Lancaster, IX.3.1966 (n = 5, emgd. IX.12 /26). 68F60: CA, San Diego Co., 1 mi. E Jacumba, VI.7.1968 (n = 6, emgd. VIII.5/28). 91F17: CA, Contra Costa Co., Antioch Natl. Wildlife Refuge (LC), VI.11.1991 (n = 1, emgd. IX.9). 91F17.1: same data except (SP, west parcel) (n = 1, emgd. IX.11).

Gutierrezia sarothrae.— all CA, San Diego Co.: 66J11: Buckman Spr., IX.2.1966 (n = 1, emgd. IX.21). 66J12: 1 mi E Boulevard, IX.2.1966 (n = 4, emgd. IX.7 to IX.26). 67K61: Lyons Vy., X.4.1967 (n = 1, dead in pupal shell). 67K71: Scissors Crossing, X.5.1967 (n = 1, emgd. X.8).

Gutierrezia sp. (sterile). - 67K30: CA, Los Angeles Co., 2 mi. N Lancaster, X.2.1967 (n = 1, dead in pupal shell). 67K60: CA, San Diego Co., Lee Vy., X.4.1967 (n = 1, emgd.). 67K65: CA, S.D. Co., Buckman Springs, X.5.1967 (n = 3, emgd. X.10/18). 67K92: CA, San Luis Obispo Co., Upper Cuyama Valley, X.6.1967 (n = 3, emgd. X.11). 68F33: AZ, Yavapai Co., 7 mi NE Bridgeport, VI.4.1968 (n = 2, emgd. VIII.16 to X). 68F36: AZ, Gila Co., Pine campgr., VI.5.1968 (n = 1, emgd. VII.17).

Isocoma tenuisecta.—68F58: AZ, Pima Co., 5 mi. SE Continental, VI.6.1968 (n = 2, emgd. IX.16,18).

Isocoma menziesii.—68H28: CA, San Diego Co., Mission Dam, VIII.26.1968 (n = 1, emgd. X.1).

Associated species: 68F58 *Inga concolorella* (Oecophorinae); 67K92 unidentified sp. (Blastobasinae); 66H13 *Isophrictis* sp. (Gelechiidae); 67K65 *Battaristis pasadenae* Keifer (Gelechiidae); 68F33, 68F60, 68H28 *Eucosma ridingsana*.

Sonia comstocki Clarke, 1952

Isocoma acradenia.—66H19: CA, Los Angeles Co., 6 mi. W Lancaster, VIII.31.1966 (n = 2, emgd. X.3/9). 67K29: CA, L. A. Co., 2 mi. N Lancaster, X.2.1967 (n = 1, emgd . X.7). 67K33: same data except 6 mi. W Lancaster (n = 16, emgd. X.6/17).

Associated species: 67K33 *Ephestiodes gilvescentella* Ragonot (Pyralidae).

Sonia filiana (Busck, 1907)

Isocoma acradenia.—all CA, San Diego Co.: 66J10: 4 mi. SE El Cajon, IX.2.1966 (n = 12, emgd. IX.13 to X.1). 67K59: same locality, X.4.1967 (n = 83, emgd. IX.18 to XII.16).67K79

Associated species: 67K79 *Amydria obliquella* Dietz (Acrolophidae); 66J10 *Isophrictis* sp. (Gelechiidae); 66J10, 67K59 *Battaristis pasadenae* Keifer (Gelechiidae); 66J10, 67K59 *Eucosma sandiego*.

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DESCRIPTION OF A NEW LEPIDOPTERAN STRUCTURE, THE ABDOMINAL TUBERCLES

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ABSTRACT. Adult moths of the superfamily Cossoidea (Lepidoptera) have been found to possess paired tuberculate evaginations on abdominal tergites 2-8. At least in Cossidae, the tubercles appear glandular based on light and scanning electron microscopy studies. Similar "abdominal tubercles" have also been found in the lepidopteran families Andesianidae, Acrolophidae, Arrhenophanidae, Brachodidae, Carposinidae, and Pyralidae. The tubercles in these other families appear non-homologous to those in Cossoidea, suggesting that these structures have arisen multiply in independent lineages. Paired tuberculate invaginations also were found on the anterior margins of abdominal tergites 2-8 on adults of Megalopygidae, but these structures appear to be non-homologous with the evaginated abdominal tubercles of the Cossoidea.

Additional key words: abdominal glands, Cossidae, Cossulinae, Cossoidea

INTRODUCTION

In the course of a revision of the cossid moth subfamily Cossulinae (in preparation), adult moths throughout the superfamily Cossoidea (Cossidae + Dudgeoneidae) were found to possess paired tuberculate evaginations on abdominal tergites 2–8 (Fig. 1). These organs apparently have not been observed previously in any insect, including Lepidoptera. Although tuberculate structures similar to those described here have been described in the Tineoidea and Copromorphoidea by Kyrki (1983) as wart-like protuberances, these structures only occur on the 2nd abdominal sternite. The purpose of the present study was to fully characterize the structure of the "abdominal tubercles" in Cossidae, where they appear to be glandular, and to explore their presence/absence across other lepidopteran superfamilies to understand their possible phylogenetic significance.

MATERIALS AND METHODS

Taxon sampling (Table 1)

Representatives of all subfamilies within Cossidae, including nearly all species of Cossulinae, were examined by light microscopy for the presence of abdominal tubercles, as were the dudgeoneid genera *Acritocera* and *Dudgeonea*. One species, *Cossula arpi* Schaus, was selected for additional study using the SEM. Light microscopy was used to examine taxa broadly sampled across the Lepidoptera. The taxa examined apart from Cossulinae (64 species representing 49 families and 26 superfamilies) are listed in Table 1, showing their positions in the current best estimate of higher phylogeny (Kristensen and Skalski 1999). In Cossulinae, all known species were examined except '*Cossula*' *abnoba* Schaus, '*Cossula*' *alboperlata* Bryk, '*Cossula*' *magna* Schaus, '*Cossula*' *manes* Druce, '*Cossula*' *ophthalmodes* Hering, and '*Cossula*' *tacita* Druce, for which no material was available. The Cossoidea currently are hypothesized to be sister group to the Sesioidea, and these in turn to be most closely related to Zygaenoidea. Multiple families of both Sesioidea and Zygaenoidea were sampled. This clade in turn falls among the unresolved basal (non-obtectomeran) groups of Apoditrysia (Kristensen and Skalski 1999), for which the four other largest superfamilies were sampled. Additional groups examined included six non-ditrysian superfamilies, all four superfamilies of non-apoditrysian Ditrysia, and nine obtectomeran superfamilies including five superfamilies and nine families of Macrolepidoptera.

Specimen preparation

Specimens from taxa outside Cossulinae were examined using slide preparations in the National Museum of Natural History, Washington, D.C., and from the Australian National Insect Collection (ANIC) at CSIRO, Canberra, Australia (slide numbers in Table 1). For Cossulinae, abdomens were dissected by placing them in 10% KOH solution for approximately 12 hours at room temperature (72 degrees F) or for approximately 10 minutes when heated on a hot plate. The abdomen then was placed in 50% EtOH/water solution and the scales removed gently from the cuticle with a fine-tipped camel hair brush. The abdomen was cut along the spiracles with dissecting scissors in order to make both the ventral and dorsal sides visible when slide-mounted. Chlorazol black stain was used for approximately 15 minutes or until sufficiently stained a light blue. After staining the abdomen was placed in 95% EtOH for 10 minutes to remove any remaining water, transferred to clove oil for 10 minutes for further clearing, and then to xylene for 10 minutes to fix the cuticle The structures were then slide-mounted in Canada balsam.

Digital photography of the tubercles was

accomplished using slide-mounted structures and Auto-Montage (Synoptics Ltd.) software, which blends multiple images taken at various focal lengths to give one completely focused image. Scanning electron microscope images were taken using an Amray 1810 with a LaB6 (lanthanum hexaboride) source.

RESULTS

Description of Tubercles

In the Cossidae, the tubercles occur in both sexes but are slightly less developed in females. The tubercles increase in size caudally (Fig. 1), with the first pair reduced to a small pore leading to an apparent internal gland (Figs 2, 8), and the caudal-most pair suberect and digitiform (Fig. 9). The anterior-most tubercles are minute, the more caudal pairs range up to approximately 0.1 mm in length (Figs 3–5), clearly visible under a dissecting microscope. In the representative of Cossulinae examined by SEM, an asymmetrical flap of tissue, possessing a fimbriate tip, extends from the apex of the tubercle (Figs 6–7).

It appeared initially that these organs were present only in Cossidae, because tubercles of similar size were seen in no other superfamily. However, upon closer inspection of the dudgeoneid genera *Acritocera* (Fig. 11) and *Dudgeonea* (Fig. 12), the tubercles were found,

TABLE 1. Lepidopteran taxa outside Cossulinae examined for the presence of abdominal tubercles. Family and superfamily nomenclature follows Kristensen and Skalski (1999) Slide numbers refer to specimens deposited at the National Museum of Natural History, Washington, D.C., and the Australian National Insect Collection (ANIC) at CSIRO, Canberra, Australia.

Superfamily	Family	Species (USNM/ANIC slide #)	Abdominal Tubercles present?
NON–DITRYSIAN SUPERFAMILIES (6 of 13 sampled)			
Micropterigoidea	Micropterigidae	*Paramartyria immaculatella* Issiki (16454, 16453)	–
		Sabatinca aurella (Hudson) (91789, 16086)	–
Eriocranioidea	Eriocraniidae	*Eriocraniella mediabulla* Davis (3241)	–
Nepticuloidea	Nepticulidae	*Ectoedemia heinrichi* Busck (16848)	–
Incurvarioidea	Incurvariidae	*Tegeticula yuccasella* (Riley) (97859, 97820)	–
Palaephatoidea	Palaephatidae	*Palaephatus pallidus* Davis (21321, 21320)	–
Andesianoidea	Andesianidae	*Andesiana lamellata* Gentili (32428, 31763)	X
		Andesiana similis Gentili (32429)	X
DITRYSIA - NONAPODITRYSIAN SUPERFAMILIES (4 of 5 sampled)			
Tineoidea	Acrolophidae	*Acrolophus popeanellus* (Clemens) (18177)	X
	Arrhenophanidae	*Arrhenophanes perspicilla* (Stoll) (23624, 23626)	X
	Psychidae	*Cryptothelea watsoni* Jones (69834)	–
	Tineidae	*Nemapogon* sp. (91883)	–
Gracillarioidea	Bucculatricidae	*Bucculatrix simulans* Braun (91984)	–
	Gracillariidae	*Caloptilia juglandiella* (Chambers) (92007)	–
		Caloptilia reticulata (Braun) (92010)	–
Yponomeutoidea	Acrolepiidae	*Acrolepiopsis incertella* (Chambers) (91672, 91666)	–
	Glyphipterigidae	*Glyphipterix bifasciata* Walsingham (77163, 77166)	–
	Ochsenheimeriidae	*Ochsenheimeria vacculella* Fischer von Röslerstamm (16126, 16138)	–
	Plutellidae	*Protosynaema eratopis* Meyrick (77666)	–
	Yponomeutidae	*Atteva punctella* (Cramer) (76651, 76661)	–
Gelechioidea	Blastobasidae	*Holocera gigantella* Chambers: slide DA 1835 (UCB)	–
		Holocera chalcofrontella Clemens (80995)	–
	Gelechiidae	*Gelechia turpella* (Denis & Schiffermüller, 1775) (6869, 6848)	–
		Gelechia versutella Zeller (86693)	–
	Glyphidoceridae	*Glyphidocera hulberti* Adamski (81243)	–
	Xyloryctidae	*Cryptophasa rubescens* Lewin (12544, 12543)	–

(continued)

TABLE 1. (continued)

Superfamily	Family	Species (USNM/ANIC slide #)	Abdominal Tubercles present?
APODYTRISIA - NON-OBTECTOMERAN SUPERFAMLIES (7 of 11 sampled)			
Zygaenoidea	Dalceridae	*Dalcera abrasa* Herrich-Schaeffer (28095, 28094)	–
		Dalcerina tijucana (Schaus) (28083, 28082)	–
	Limacodidae	*Acharia helenans* Dyar (slide numbers absent)	–
	Megalopygidae	*Megalopyge defoliata* Walker (28095)	–
	Zygaenidae	*Illiberis sinensis* Walker (12142, 12140)	–
Cossoidea	Cossidae	*Archaeoses polygrapha* (Lower) (H 28)	X
		Charmoses dumigani Turner (PG 907)	X
		Cossodes lyonetii White (96148)	X
		Idioses littleri Turner (PG 909, PG 910)	X
		Ptilomacra senex Walker (96149)	X
	Dudgeoneidae	*Acritocera negligens* Butler (ANIC 1550)	X
		Dudgeonea sp. (ANIC 2550)	X
Sesioidea	Brachodidae	*Brachodes appendiculatus* (Esper) (77547, 77548)	X
		Brachodes canonitis Meyrick (77592)	X
	Castniidae	*Telchin licus* (Drury) (96147)	–
	Sesiidae	*Alcathoe autumnalis* Engelhardt (75719)	–
		Paranthrene simulans (Grote) (75792, 75791)	–
Choreutoidea	Choreutidae	*Prochoreutis inflatella* (Clemens) (77118, 77119)	–
Tortricoidea	Tortricidae	*Phricanthes asperana* Meyrick (89912)	–
Alucitoidea	Alucitidae	*Alucita* sp. (63644)	–
Pterophoroidea	Pterophoridae	*Paraplatyptilia shastae* (Walsingham) (63247, 63248)	–
OBTECTOMERA - NON-MACROLEPIDOPTERAN SUPERFAMILIES (4 of 6 sampled)			
Copromorphoidea	Carposinidae	*Carposina nipponensis ottawana* Kearfott (22325)	X
	Copromorphidae	*Lotisma trigonana* (Walsingham) (77115, 77069)	–
Hyblaeoidea	Hyblaeidae	*Hyblaea puera* (Cramer) (107522, 110219)	–
Pyraloidea	Crambidae	*Maracayia chlorisalis* (Walker) (104689, 104684)	–
	Pyralidae	*Condylolomia participalis* Grote (106364, 104464, 104465)	X
Thyridoidea	Thyrididae	*Meskea dyspteraria* Grote (107524, 107528)	–
MACROLEPIDOPTERAN SUPERFAMILIES (5 of 11 sampled)			
Bombycoidea	Sphingidae	*Eumorpha achemon* (Drury) (3723)	–
Lasiocampoidea	Lasiocampidae	*Tolype velleda* (Stoll) (40969)	–
		Tolype minta Dyar (40967)	–
Drepanoidea	Drepanidae	*Drepana arcuata* (Walker) (56418, 56420)	–
Geometroidea	Geometridae	*Prochoerodes forcicaria* (Guenée) (56692, 56693)	–
	Uraniidae	*Psamathia placidaria* (Walker) (57164, 57165)	–
Noctuoidea	Arctiidae	*Halysidota ata* Watson & Goodger (57065, 38264, 38265)	–
	Lymantriidae	*Orgyia vetusta* Boisduval (52411, 52410, 52407)	–
	Noctuidae	*Cissusa valens* (Edwards) (40504, 40505)	–
		Papaipema furcata (Smith) (39418)	–
	Notodontidae	*Macrurocampa dorothea* Dyar (2765, 2714)	–

but they are much smaller than in most Cossidae. Some genera considered to be among the most primitive cossids (E. D. Edwards, pers. comm.) also were found to have small tubercles like those in *Dudgeonea* and *Acritocera*, including *Archaeoses* (Fig. 13), *Idioses*, and *Charmoses*, whose subfamily affinities are currently in doubt (Edwards 1996). The tubercles in Dudgeoneidae are approximately 0.01 mm in length and can be only seen with a compound microscope. Although similar in form to the tubercles in Cossidae, including the presence of a terminal pore, they are relatively uniform in size among abdominal segments.

In addition to Cossoidea, abdominal tubercles were observed (Table 1) in all representatives examined from Andesianidae (Figs 14–15), Acrolophidae (Figs 16–17), Arrhenophanidae (Figs 18–21), Brachodidae (Figs 22–23), Carposinidae (Fig. 24), and Pyralidae (Figs 25–26). These tubercles are similar in size to those in Dudgeoneidae, but differ in apparently lacking the terminal pore seen in Cossoidea.

Examination of the megalopygid species *Megalopyge defoliata* revealed paired tuberculate invaginations (as opposed to the evaginate tubercles described above) on the anterior margin of each abdominal sclerite (Figs 27–30). These invaginations are approximately 0.1 mm long and lack an apical pore. Occasionally one member of the pair can be missing from a given segment.

DISCUSSION

The function of the abdominal tubercles is unknown, but several observations suggest that, at least in Cossidae, they may be glandular. First, the tubercles in cossids possess an internal canal which opens to the outside through a terminal pore. Second, at the base of the tubercle (e.g. Fig. 9) there appears to be an enclosed chamber, plausibly interpreted as a gland. Third, the fimbriate tip of the tubercle seen under SEM is suggestive of an evaporative surface. Because the tubercles in Cossidae are so small, and occur in both sexes, it is unlikely that they are associated with long-range pheromone production. It seems more plausible that they could be involved in production of a close range pheromone, or a defensive chemical (Hallberg and Poppy 2003). Clearly, histological, physiological, and behavioral studies will be required to test these hypotheses.

From their distribution across major lepidopteran lineages (Table 1), it appears that abdominal tubercles have arisen sporadically in multiple, independent groups. With the possible exception of Brachodidae (see below), it seems unlikely that the tubercles in Cossoidea represent shared ancestry with any occurrences outside that superfamily. Lack of a terminal pore in tubercles outside Cossoidea further suggests non-homology of these. The paired invaginations found in Megalopygidae seem especially unlikely to be homologous to the other tubercles observed, which are never invaginations, but are rather evaginations from the abdomen.

While sampling outside Cossoidea was very sparse, these preliminary observations suggest that presence of abdominal tubercles might prove to be a phylogenetically informative character within several families and/or superfamilies when sampling is expanded. For example, tubercles were found in some but not all of the families examined within Tineoidea, and within Copromorphoidea and Pyraloidea as well.

If we accept the monophyly of Cossoidea (Edwards et al. 1999), it follows that the shared possession of tubercles is inherited from the ancestor of Cossidae and Dudgeoneidae. However, it is unclear whether this trait is a synapomorphy for Cossoidea. Recent evidence suggests that the sister group to Cossoidea is Sesioidea, within which the family relationships appear to be (Brachodidae (Sesiidae,Castniidae)) (Edwards et al. 1999). In Sesioidea, tubercles appear to occur only in Brachodidae. It is possible that this is an independent origin from that in Cossoidea. However, assuming that further sampling confirms that tubercles belong to the groundplan of Brachodidae, it would be equally parsimonious to assert that the tubercles arose in the common ancestor of the two superfamilies, and were subsequently lost in the sesiid/castniid lineage. There is no obvious way to distinguish these alternatives.

Within Cossoidea, variation in the development of the abdominal tubercles may provide a synapomorphy for a majority of Cossidae. As noted earlier, small and uniform-sized tubercles, the condition in Dudgeoneidae, are also found in several Australian genera thought to be primitive within Cossidae (E. D. Edwards, pers. comm.). Thus, the enlargement of the tubercles on the caudal abdominal segments in most genera of Cossidae may be a derived condition. Further study of cossid phylogeny is needed to test this hypothesis.

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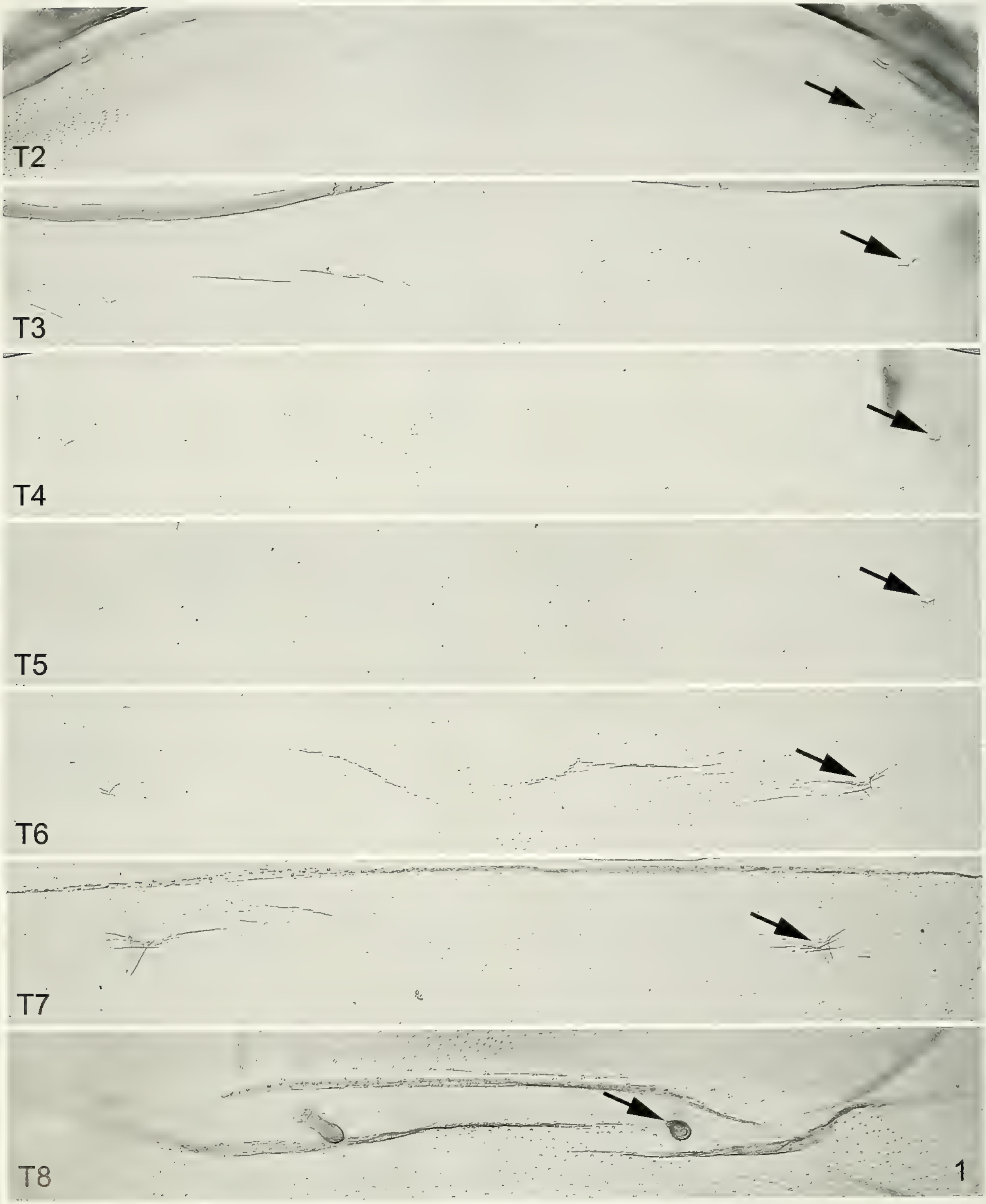
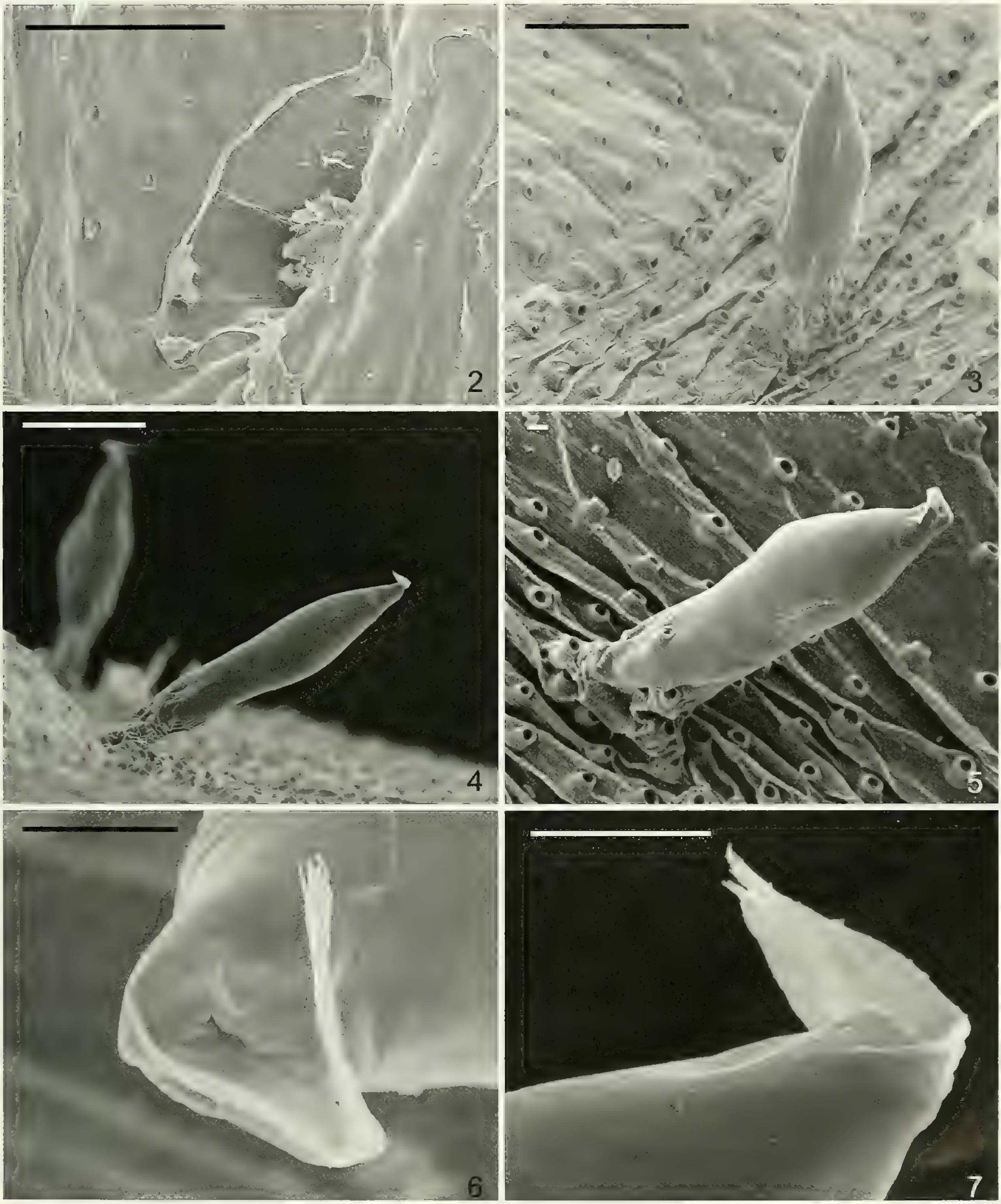
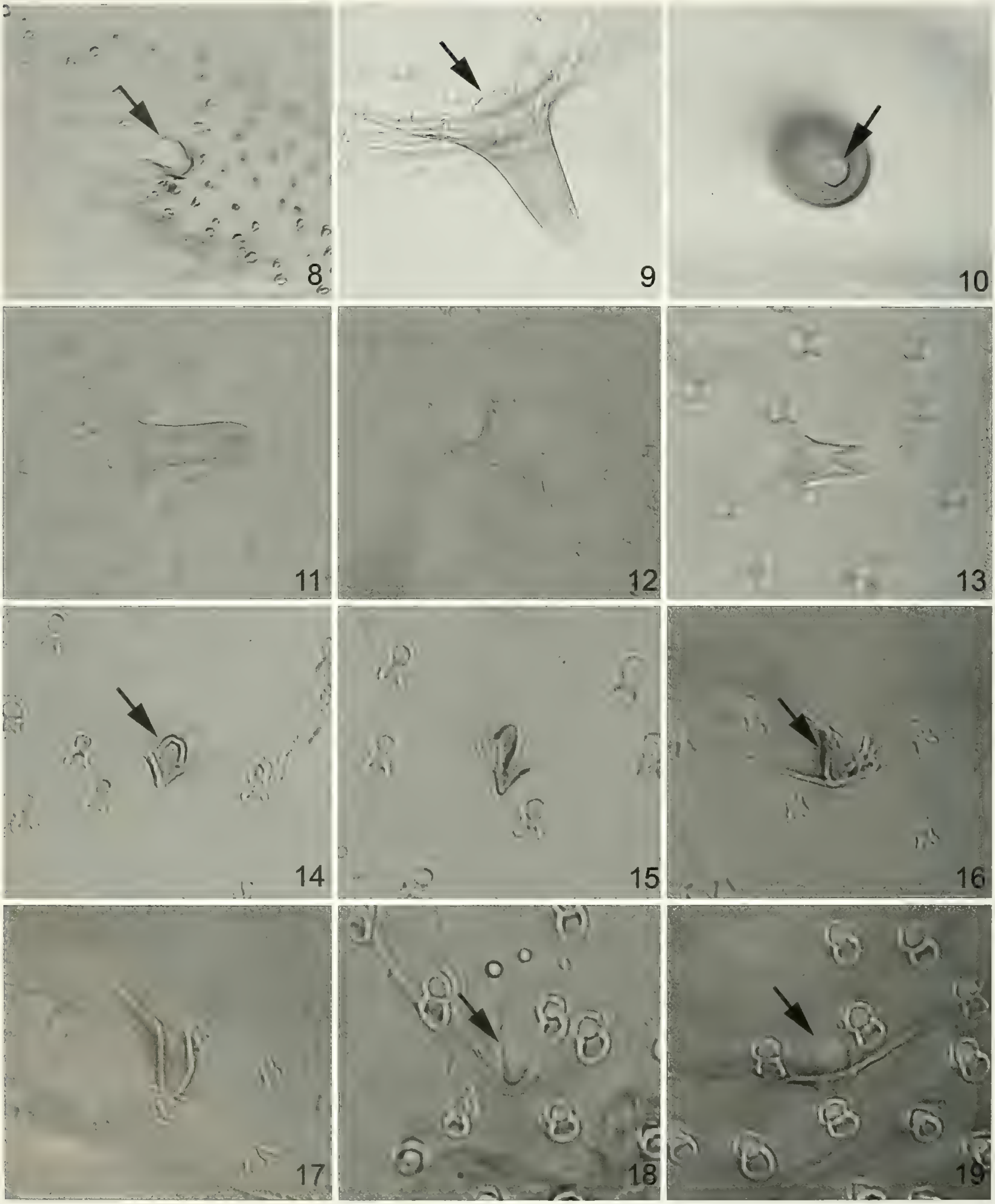


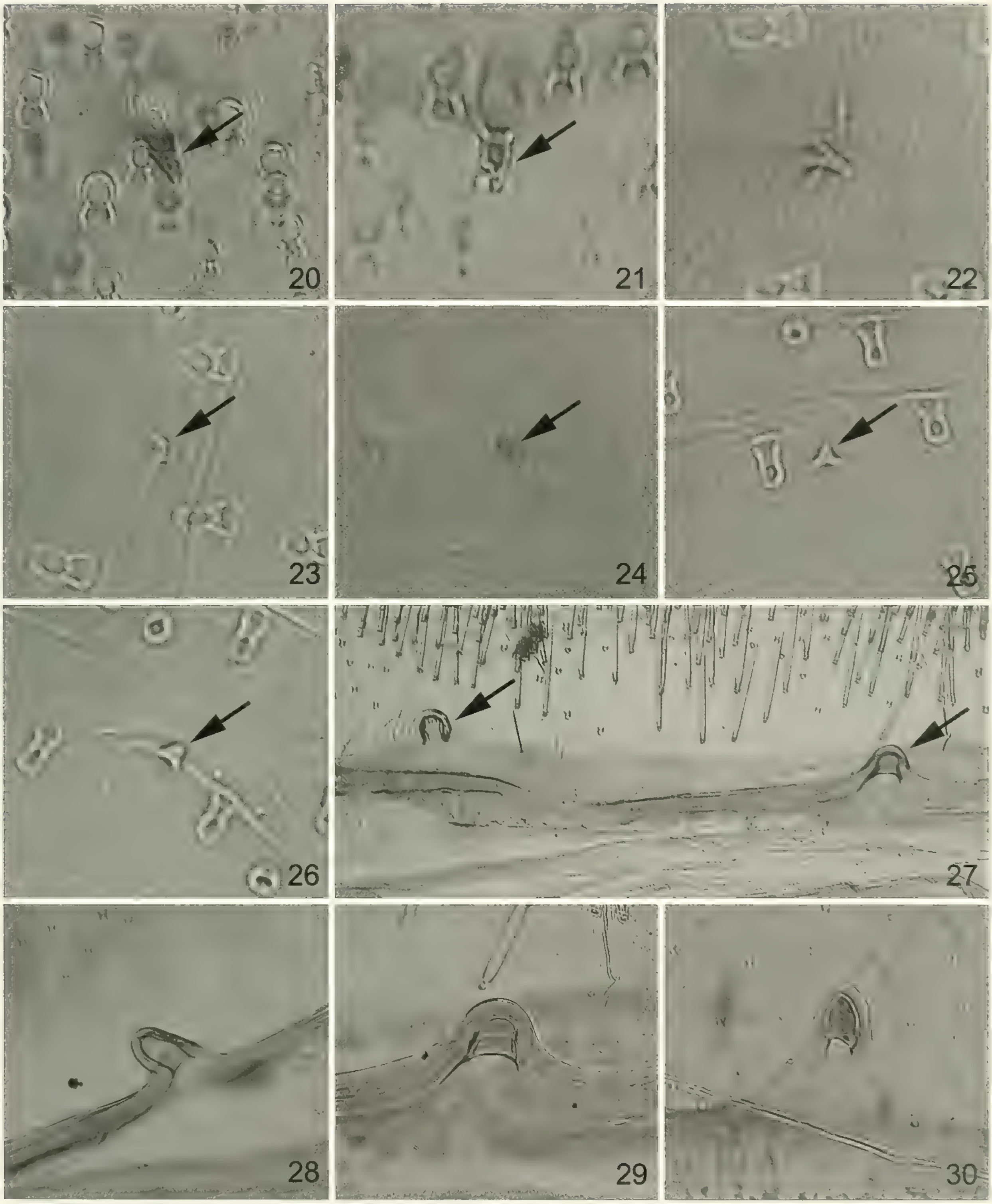
FIG. 1. Abdominal tubercles of *Cossula arpi*.



FIGS. 2-7. Abdominal tubercles. Cossidae, *Cossula arpi*: 2, SEM of interior of tubercle; 3, SEM of tubercle on tergite 7; 4, SEM of tubercles on tergite 7; 5, SEM of tubercle on tergite 7; 6, enlargement of apex of tubercle in 5; 7, enlargement of apex of tubercle in 4.



FIGS. 8-19. Abdominal tubercles. Cossidae, *Cossula arpi*: 8, tubercle on tergite 2; 9, tubercle on tergite 6; 10, tubercle on tergite 8. Dudgeoneidae, *Acritocera negligens*: 11, tubercle on tergite 5; *Dudgeonea* sp: 12, tubercle on tergite 6. Cossidae, *Archaeoses polygrapha*: 13, tubercle on tergite 6. Andesianidae, *Andesiana lamellata*: 14, tubercle on tergite 4; 15, tubercle on tergite 5. Acrolophidae, *Acrolophus popeanella*: 16, tubercle on tergite 4; 17, tubercle on tergite 5. Arrhenophanidae, *Arrhenophanes perspicilla*: 18, tubercle on tergite 2; 19, tubercle on tergite 4.



FIGS. 20-30. Abdominal tubercles. Arrhenophanidae, *Arrhenophanes perspicilla*: 20, tubercle on tergite 4; 21, tubercle on tergite 5. Brachodidae, *Brachodes canonitis*: 22, tubercle on tergite 4; 23, tubercle on tergite 6. Carposinidae, *Carposina nipponensis*: 24, tubercle on tergite 4. Pyralidae, *Condylolomia participalis*: 25, tubercle on tergite 2; 26, tubercle on tergite 5.Megalopygidae, *Megalopyge defoliata*, tuberculate invaginations: 27, tubercles on tergite 4; 28, tubercle on tergite 3; 29, tubercle on tergite 4; 30, tubercle on tergite 5.

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LIFE HISTORY AND BIOLOGY OF *FORBESTRA OLIVENCIA* (BATES, 1862) (NYMPHALIDAE, ITHOMIINAE)

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ABSTRACT. *Forbestra* is the only mechanitine genus lacking a thorough life history description and little is known of its biology. Accordingly I describe the immature stages including first instar chaetotaxy, and provide observations on the biology of *Forbestra olivencia* from Garza Cocha in eastern Ecuador. Morphological characters from the early stages of *Forbestra olivencia* are identified that are unique to *Forbestra* and support the close relationship of *Forbestra* and *Mechanitis*. *Forbestra olivencia* was a moderately common butterfly at Garza Cocha during the sample period, far outnumbering other sympatric *Forbestra*. Ecological observations demonstrate similarities between *F. olivencia* and *Mechanitis*, but suggest *F. olivencia* is more restricted to shaded microhabitats.

Additional key words: Mechanitini, *Mechanitis*, chaetotaxy

INTRODUCTION

Ithomiine butterflies have played an important role in the development of mimicry theory, having been the original models of imitation described by Bates (1862). In that paper Henry Bates described *Mechanitis olivencia* based on wing color pattern differences being consistently different from other sympatric *Mechanitis* in the western Amazon basin. Forbes (1924) noted characters of the color pattern, wing venation, and male genitalia that distinguished "*equicola* and allies" from "*polymnia* and allies". Fox (1967) erected the genus *Forbestra* to contain "*equicola* and allies", including *olivencia*, and identified characters of the female forelegs as distinct from *Mechanitis*. In the 40 years since its description little has been published on the biology of species in the genus *Forbestra*, despite their being among the larger and more conspicuous ithomiines.

Recent systematic work on ithomiines has used characters from the early stages in phylogeny reconstruction (Brown & Freitas 1994, Motta 2003), making use of the fact that life history data are available for nearly all genera. Photographs of larvae and pupa of *F. equicola* (Cramer) (Brévignon 2003) and a brief description and drawing of the larva of *F. olivencia* by Drummond (1976) are all the life history information that exists for *Forbestra*. Moreover, *Forbestra* is the only genus lacking a thorough life history description in the tribe Mechanitini (Freitas & Brown 2002), a group comprised of several mimetic color patterns and thus of interest for the evolution of mimicry. Accordingly, I describe the early stages of *Forbestra olivencia juntana* (Haensch) from eastern Ecuador, and include in the descriptions characters developed for phylogeny reconstruction (Brown & Freitas 1994, Motta 2003). In addition, I report observations on the ecology, behavior and morphology of *Forbestra olivencia*.

MATERIALS AND METHODS

Observations were made intermittently between 2000-2005 at Garza Cocha (S 00°29.87', W 76°22.45'), Provincia Sucumbios, Ecuador. Early stages were reared in plastic cups and plastic bags under ambient conditions (22-30° C, 70-100% relative humidity) in a wood building with screen windows. During the drier parts of the year (December to February) larvae were moved daily from the building to a shaded environment under a nearby building to maintain ambient conditions. Observations were recorded daily and head capsules and pupal exuviae were collected. Larval specimens were boiled and subsequently stored and studied in 70% ethanol and deposited in the author's collection. First instar head capsules were treated with 10% KOH to dissociate the mandibles and labrum. Host plant vouchers were collected and deposited in the Herbario Nacional de Ecuador (voucher number: RIH-596).

Observations on adults were made at the same locality in the surrounding forest. Adults were marked and released, or collected for other studies. I recorded flight height, microhabitat conditions, and adult diet. Forewing length was measured with digital calipers and body mass was measured with a portable balance (Acculab) accurate to 1 mg. Ithomiine taxonomy follows Lamas (2004), except that *Mechanitis messenoides* Felder & Felder is treated as a species, rather than a subspecies of *M. mazaeus* Hewitson, based on observed differences in host plants, color pattern and DNA sequence data at this site (unpublished).

RESULTS

Early Stage Biology

Host plant. Host plant specimens were compared with material in the Herbario Nacional de Ecuador and determined to be *Solanum monarchostemon* Knapp, and Michael Nee of the New York Botanical Garden

confirmed the determination. *Forbestra olivencia juntana* were only found using *S. monarchostemon* at Garza Cocha. However, Elias and Willmott (pers. comm.) observed *F. olivencia* using *Solanum thelopodim* Sendtn., in addition to *S. monarchostemon*, south of the Rio Napo near Añangu.

It should be noted that the host of *F. olivencia* recorded at Limoncocha is not *Solanum anceps* Ruiz. & Pav. as reported in Drummond (1976) and Drummond & Brown (1987). The host specimen (Drummond 7315) listed in Drummond (1976) was studied by Knapp (2000) and determined to be *S. monarchostemon*.

Solanum monarchostemon was found in primary forest in well-drained, well-lit areas and associated with gaps. Individuals hosting *F. olivencia* were 0.5 - 1.3 m tall, often with flowers and/or fruits, and found in shaded areas near gaps, but not at gap edges or in gaps. A group of six *Mechanitis messenoides* eggs was found on *S. monarchostemon* and reared to be normal sized adults.

Ants were commonly found patrolling *Solanum monarchostemon*. *Ectatomma*, *Crematogaster*, *Wasmannia*, *Camponotus* (identified using Bolton 1994), and three unidentified genera were collected from the hosts. *Crematogaster* were observed attacking and carrying away *F. olivencia* eggs on one host. *Ectatomma* and other genera were not observed interacting with eggs or larvae, and one female *F. olivencia* oviposited on a host with *Ectatomma* present. In addition to ants, an unidentified species of braconid wasp was observed searching *S. monarchostemon* and larvae of a different braconid species emerged from 4th instar *F. olivencia*.

Oviposition. Eggs are laid on the upper leaf surface, but one egg was observed on the host plant main stem. Eggs were found laid singly (n=7), in pairs (n=11), and occasionally in clusters of three (n=3) or four (n=3). One group of eight eggs was also found. Host plants were commonly found with eggs on more than one leaf (9 out of 13 plants), commonly two of the larger host leaves. Eggs were found on small to large mature host leaves with little to extensive herbivore damage. As mentioned above, eggs and larvae were not found on plants in or bordering gaps.

Two oviposition events were observed at 11:00 and 14:30 respectively, and females were observed searching for hosts between 11:00 and 16:00. Females search the host very carefully for several minutes, hovering in front of leaves and main stem, inspecting both top and bottom of leaves and also descending slowly nearly to the ground while facing the main stem, then ascending to leaf height. Upon settling on a host leaf the female tests with antennae and touches her abdomen several times to the host leaf surface. Host assessment took nearly 10 minutes for one female, and females take one to several minutes between laying each egg. Both females first laid a pair of eggs close together, then a single egg on a different leaf.

Description of early stages: **Egg**. Fig. 1A. Duration: 4 (n = 1) to 5 days (n = 15). Mean egg height 1.59 mm, mean width 0.87 mm, with mean axes ratio (height/width) of 1.83 (n = 3). The egg is white, taller than wide, widest in middle, tapering apically to narrow but rounded apex. Egg surface sculptured with 13-17 horizontal ridges (n = 4) and 13-15 vertical ridges (n = 4) making four-sided cells with inner corners rounded off (Fig. 1A). The four-sided cell pattern changes to pentagonal and hexagonal cells near apex.

1st instar. Fig. 1B and Fig. 2. Duration: 2 days (n = 15) to 3 days (n = 6). Mean head capsule width = 0.54 mm (n = 14). Head capsule black. Body sparsely covered with dark setae. Body is pale translucent with blue tints at either end, blue palest in posterior. Body pale laterally with yellow tints and dorsum gray to green where plant material visible. Anterior of segment T1 whitish. Rounded lateral protuberance present on abdominal segments A1-8. Dorsum traversed by subtle fleshy wrinkles. Segment A10 with dark anal plate. Thoracic legs are dark. Prolegs pale with dark patch at base and A10 proleg base darker than others. Newly hatched larvae eat one to three quarters of eggshell (n = 4) or whole eggshell (n = 3). Rest with body straight on underside of leaf along secondary or tertiary leaf veins, or near hole in leaf. Larvae sometimes eat into leaf around themselves making an isolated patch of host to rest on (see Fig. 1B).

Because characters based on first instar morphology have proven informative for ithomiine phylogeny (Brown & Freitas 1994, Motta 2003), and *Forbestra* was missing in Motta's (2003) analysis, I provide a detailed description of the first instar chaetotaxy in the Appendix. The description focuses on Motta's (2003) morphological characters so the description may be used for phylogenetic analyses. The description is based on two preserved first instars and three first instar head capsules. Arrangement and relative lengths of first instar body setae are shown in Fig. 2.

2nd instar. Fig. 1C. Duration: 1 day (n = 2) to 2 days (n = 13). Mean head capsule width = 0.74 mm (n = 17). Like previous instar with the following changes. Body less translucent and pale to pale-yellow laterally. T1 is pale dorsally with blue tints, and fits snugly with posterior of head capsule. Aorta is visible dorsally. Middle body segments dorsally gray-green where food visible. Posterior to A6-7 the dorsum is pale to yellowish turning bluish on A8-9. Lateral protuberance on A3-6 rounded, those on A1-2 and A7-8 are more pointed and larger, with those on A1-2 largest. Thoracic legs and prolegs are pale with thoracic legs darker than prolegs. One individual observed eating circle into leaf around itself on underside of leaf. Commonly rest on leaf underside with body straight, lying along a secondary vein with head away from leaf midvein.

3rd instar. Fig. 1D. Duration: 2 days (n = 11). Mean head capsule width = 1.06 mm (n = 12). Like previous instar with the following changes. Thorax dorsum nearly white in anterior of T1 turning blue in posterior T1, then fades to gray in T3. Thorax is white laterally. Rest of body grayish dorsally, turning blue again on A8-9. Segment A10 white dorsally and laterally. Lateral abdominal protuberances yellowish in color, except for on A8, which is white. Lateral protuberances are rounded triangles with A1-2 longest and thinner than rest. Ventrally pale translucent. Rest on underside of leaf on midvein with body straight. When disturbed raise head and thorax off leaf substrate maintaining straight posture.

4th instar. Fig. 1E. Duration: 2 days (n = 11). Mean head capsule width = 1.44 mm (n = 9). Like previous instar with the following changes. A pair of small dorsal humps present on T1. T1-2 blue dorsally and laterally. Anterior of T3 faint blue dorsally, fading to light gray. T3 pale yellow laterally. A1-7 yellowish gray dorsally. A8-10 blue dorsally, with A10's posterior fading to pale. Lateral protuberance on A1-2 tapering to thin fleshy projection about twice as long as those on A3-A8. A3's lateral protuberance longest of A3-6 but shorter than A7-8. A1-7 lateral abdominal protuberances yellowish,

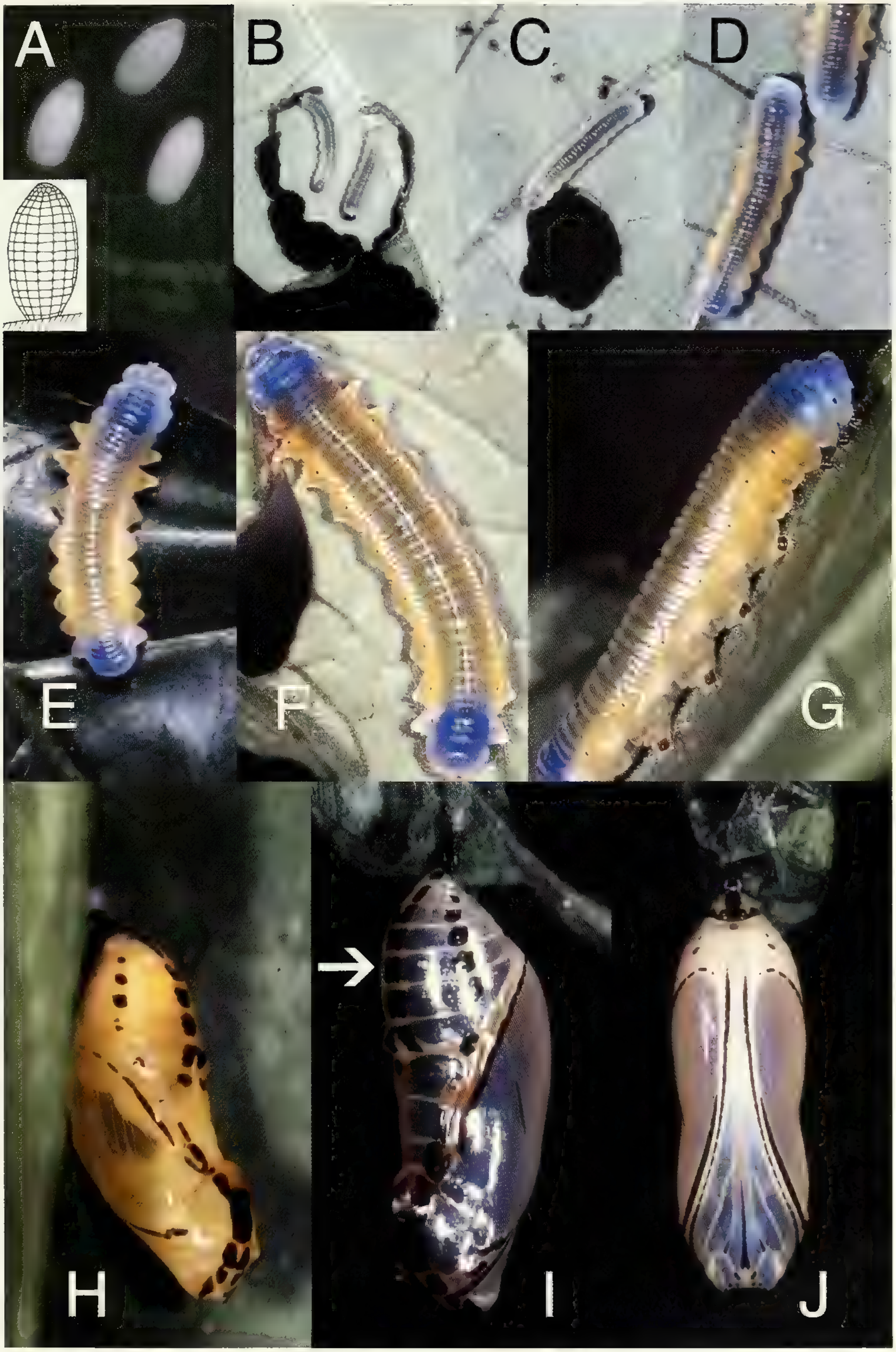

FIGURE 1. *Forbestra olivencia* life history. **A**. Leaf-top cluster of 3 eggs (image is a composite of two photos of same clutch of eggs), inset is egg drawn from specimen after storage in 70 % ethanol. **B**. First instar. **C**. Second instar. **D**. Third instar. **E**. Fourth instar. **F**. Fifth instar. **G**. Lateral view of fifth instar showing dark thoracic legs and dark patches on prolegs 3-6. **H**. Pupa with first day coloration. **I**. & **J**. Final pupa coloration in dorsolateral (I) and ventral view (J).

yellow strongest on A1-2 and A6-7. A8's lateral protuberance is pale. White stripe present on dorsal midline of abdomen. White dorso-lateral stripe present above abdominal protuberance on segments A3-6, then fading on A7. Rest on leaf underside with head down and body straight. At rest, head capsule partly obscured in dorsal view by T1. Feed from leaf margin near its apex. Braconid wasp larvae emerged from 4th instars and resulted in larval mortality.

5th instar. Fig. 1F and G. Duration: 4 days (n = 7) to 5 days (n = 3). Mean head capsule width = 2.00 mm (n = 4). Like previous instar with the following changes. Head capsule black with pale pubescence, sutures visible as light lines, and labrum light gray. T1's dorsal fleshy humps more pronounced. T1-2 blue dorsally and laterally. T3 dorsally darker than T1-2, and pale yellow laterally. A7 posterior is blue dorsally. Dorsum of A8-9 blue, but A10's whitish. Abdomen segments A1-7 yellow laterally including lateral abdominal protuberances, yellow extending onto dorsum. A8-A10 pale laterally. White dorso-lateral stripe above lateral protuberance starting in posterior of A2 and ending in anterior of A7 (mainly on A3-6). Lateral protuberances of A1-2 and A7 with white tips. Lateral protuberance of A3-8 triangular to broadly triangular. Protuberance on A1-2 twice the length of those on A4-6. A3, A7, and A8 with slightly longer more pointed protuberances than those of A4-6. Spiracles obvious and dark on T1, A1-8. Dorsum with central white to yellowish line over aorta from posterior T3 to A7. Aorta visible dorsally, and appears pale T3-A7 and dark on T2 and A8-9. Thoracic legs are black. Prolegs have dark gray to black sclerotized plate near base, this not strongly sclerotized on A6 and A10 in some individuals. Prolegs with pale pubescence near base. Pale translucent ventrally with tracheae visible. Day before pupation body turns very yellow and blue of body fades. When disturbed tuck head capsule under T1, totally obscuring head capsule dorsally. Rest head down on underside of leaf with head near where eating at margin. Larvae in groups of 2-4 stay together in all instars and no cannibalism was observed.

Pupa. Fig. 1H, I and J. Duration: 8 days (n = 9). Reflective metallic, elongate and pendant. At first all yellow without any black markings other than cremaster. Within first 24 hours black marks develop on yellow pupa (Fig. 1H) followed by yellow turning to silver with gold highlights (Fig. 1I and 1J). Cremaster black. Ventral black line extending from cremaster to region between segments A8 and A9 with pair of bumps, and there expanding laterally, overall making an anchor-shaped patch. Anterior to anchor-shaped patch, ventral abdominal midline with small faint black spots that are absent in some individuals. Ventro-laterally, abdomen has pair of black flecks on segments A5-6, segment A6's smaller. Spiracles outlined in large squarish black spots on segments A3-8, decreasing in size toward cremaster. Abdomen dorsum with series of eight squarish black spots that are separated into pairs on segments A2, A8, A9, partially fused on segments A3 and A7 and completely fused forming one large spot on segments A4-6 (arrow in Fig. 1I). A few individuals had dorsal black spots incompletely fused on A6. Together this pattern makes an elongate narrow "X", with arms of "X" more widely separated at anterior end. In between dorsal abdominal segments colored orange-brown. Transverse ridge present in anterior of A3 making a small shelf. Antennae edged in black line that is broken into dashes in middle third only. Wing pad edged black ventrally fading completely after mid-length. Wing pad edged brown and black dorsally turning to dashed black line and ending near apex. Wing pad marked only with thin black line near center. Thorax weakly keeled. Thoracic dorsum colored with broad black stripe that splits around a brown patch in posterior. Anterior to black band of keel are two black rounded squares. Additional pair of black squares located at base of antennae, and black triangles present on slightly pointed ocular caps. The day before eclosion bluish tints develop, then wing pad margin develops distinct black before the wing colors finally show through.

Adult Biology: In 204 days of fieldwork at Garza Cocha between July-August 2000, May-July 2001, May-July 2002, January-February 2003 and December 2004-January 2005, 83 individuals of *F. olivencia* were seen (recaptures excluded), 68 of which were captured and sexed (21 males, 47 females). *F. olivencia* ranked 13th in abundance out of 56 ithomiine species in the overall rank-abundance distribution of capture data during this period. *F. olivencia* was much more common than *Forbestra equicola* during the study period (*F. equicola* ranked 40th with 6 individuals), and a single *F. proceris* (Weymer) was captured outside the study period in June 2005. With respect to other mechanitines, *F. olivencia* tied *Mechanitis mazaeus* in abundance and was more common than other *Mechanitis*. *F. olivencia* was less common than *Scada zibia* (Hewitson) (11th in rank abundance with 99 individuals) and more common than *Thyridia psidii* (Linnaeus) (46th in rank abundance with two individuals). Among ithomiines with similar mimetic 'tiger' coloration (Beccaloni 1997), *F. olivencia* was the third most abundant species.

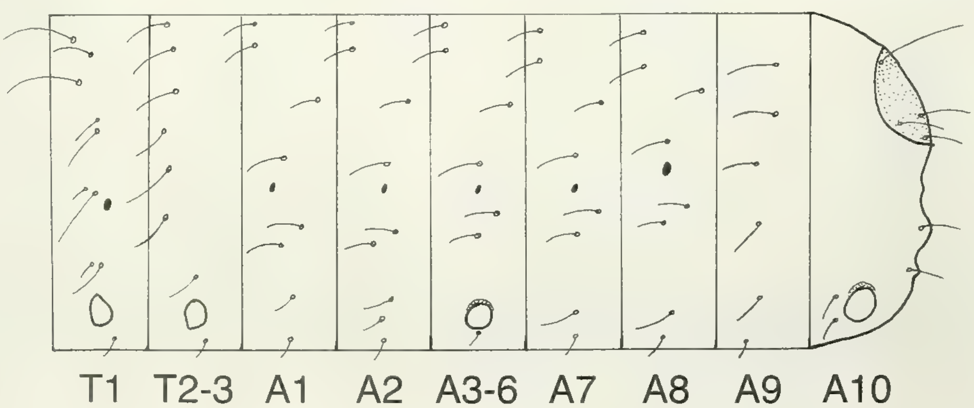

FIGURE 2. First instar body chaetotaxy. Setae drawn to represent relative lengths.

Forbestra olivencia was lowest in abundance in July-August 2000 with only four individuals (0.11 individuals per day) and more common in other sampling periods with 13 individuals during May-July 2001 (0.23 individuals per day), 25 individuals during May-July 2002 (0.47 individuals per day), 19 individuals during January-February 2003 (0.76 individuals per day), and 22 individuals during December 2004-January 2005 (0.62 individuals per day).

Forbestra olivencia inhabits primary forest. Females are commonly seen flying in the understory with a mean flight height above the ground of 1.0 m (n = 39, s.d. = 0.63). Males were observed flying higher than females at a mean height of 1.6 m (n = 20, s.d. = 0.86; unpaired *t*-test, $t = -2.7$, $P = 0.009$). Individuals were observed only in shaded forest or near small forest gaps. Although no individuals of *F. olivencia* were observed in open areas, *F. proceris* was observed visiting Asteraceae flowers in a cleared field.

Observed adult resources of *F. olivencia* at Garza Cocha include bird droppings, and rarely splattered fruit or other leaftop detritus. *F. olivencia* females visit bird droppings (n = 5; Fig. 3A), and were observed flying in the immediate vicinity of army ants (*Eciton* spp.) stopping at white fungal patches on leaves and bird droppings. One male was observed feeding on bird droppings. No *F. olivencia* were observed visiting Asteraceae flowers or other pyrrolizidine alkaloid sources during this study.

F. olivencia is sexually dimorphic with respect to size. Forewing length of wild-caught females (mean = 33.88 mm, s.d. = 2.30 mm, N = 27) is significantly longer than wild-caught males (mean = 31.97 mm, s.d. = 2.64 mm, N = 14; unpaired *t*-test, $t = 2.40$, $P = 0.021$). However female body mass (mean = 72 mg, s.d. = 19 mg, N = 20) is not significantly higher than males (mean = 65 mg, s.d. = 21 mg, N = 11; unpaired *t*-test, $t = 0.99$, $P = 0.3$). Mating takes place during the middle of the day as a pair was seen in copula at 13:00 with the smaller individual, presumably male, flying. Forewing length of reared females (mean = 32.80, s.d. = 0.85, n = 4) and males (mean = 31.33, s.d. = 1.88, n = 4) did not differ from wild-caught individuals of the same sex (unpaired *t*-test, $t = 0.91$, $P = 0.37$ for females, and $t = 0.45$, $P = 0.66$ for males).

DISCUSSION

The genus *Forbestra* ranges throughout the Amazon basin and Lamas (2004) recognizes three species (*F. equicola*, *olivencia*, and *proceris*). *Forbestra* species participate in "tiger" mimicry complexes with other ithomiines and heliconiines (Beccaloni 1997, Brown 1988). These species exhibit a combination of orange hind wing with transverse black bar, and forewing with orange, yellow and black oblique stripes (Fig. 2).

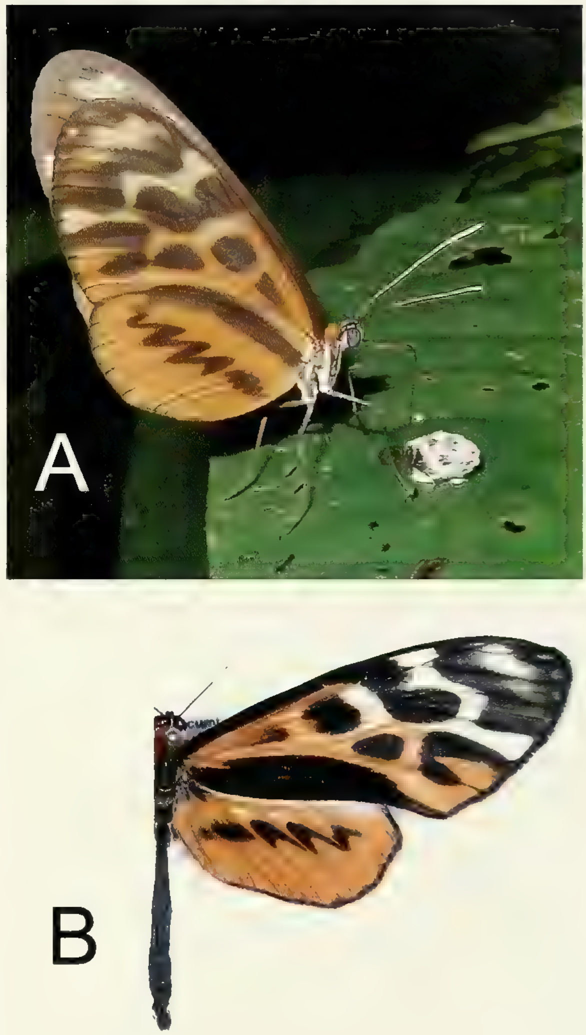

FIGURE 3. Adult *F. olivencia juntana*. **A**. Ventral wing pattern of female feeding on bird dropping. **B**. Dorsal wing pattern of male reared from larva.

Morphology of *Forbestra olivencia* early stages provides useful characters to identify *F. olivencia*, and corroborates both the generic status of *Forbestra* and the sister relationship between *Mechanitis* and *Forbestra*. Characters of first instar chaetotaxy developed for phylogenetic analysis described in this study (Appendix) are not discussed further. In addition to *F. olivencia*, data for *Sais rosalia* were lacking from Motta's (2003) analysis, and were not included in Freitas and Brown's (2002) description of *Sais rosalia* early stages. Thus comparison of first instar chaetotaxy for all genera of Mechanitini was not undertaken here.

Two characters of *F. olivencia* early stages appear unique to this species. First, the pupa has dorsal black abdominal spots that make a narrow "X" and completely merge only on A4 - 6 (arrow in Fig. 1I). *F. equicola*'s black abdominal spots merge on A4 - 8 and no data on the immatures of *F. proceris* are yet available. Second, *F. olivencia* larvae have elongate lateral protuberances on A1-2 reminiscent of those along the abdomen of *Mechanitis*. Such protuberances are not present on *F. equicola* (Brévignon 2003). However, these elongate lateral protuberances may be variable as Drummond's (1976) larval drawing of *Forbestra olivencia juntana* (called *F. truncata juntana*) from Limoncocha lacks elongate protuberances on A1-2.

Like *Mechanitis*, *F. olivencia* lays eggs on leaf tops. However, *F. olivencia* typically lays eggs singly or in small clusters of 2 - 4 and not large clusters as in *Mechanitis*. Although there is no information on *F. equicola* egg clutch size in Brévignon (2003), the fact that the larvae are together on a single leaf suggests *equicola* also lays eggs in groups of small size (~ 6). Thus the genus *Forbestra* appears to lay eggs in smaller clutches than *Mechanitis* and additional observations on *Forbestra* species would clarify whether there are consistent differences between these genera.

The pupa of *Forbestra olivencia* is strikingly similar to *Mechanitis messenoides* and *M. mazaeus* at Garza Cocha (unpublished). *F. olivencia* pupae differ from those of *Mechanitis* primarily in the arrangement of the rows of black dorsal abdomen spots. In *F. olivencia* these spots completely join on segments A4 - 6 making an "X" (arrow in Fig. 1I), and in *F. equicola* they are fused on A4 - 8 and separated on A2-3. In *M. messenoides* and *M. mazaeus* (and *M. polymnia* Fox 1967, Fig. 7) the spots come close together on segments A4 - A6 but do not join and other mechanitine genera have them located more subdorsally (Brown & Freitas 1994, Fig. 4F and A. Freitas pers. comm.). Thus, in addition to genitalia, wing and leg characters (Forbes 1924 and Fox 1967), the dorsal fusion of these spots on A4 - 6 is likely a synapomorphy for *Forbestra*.

The close relationship between *Forbestra* and *Mechanitis* recognized by Bates (1862), Forbes (1924), and Fox (1967) is supported by characters of the immature stages (Brown & Freitas 1994, Fig. 1A) as well as DNA sequence data (Brower et al. 2006). Synapomorphies from the immature stages (excluding 1st instar chaetotaxy) supporting this relationship identified by Freitas and Brown (1994) and corroborated here include: egg axes ratio > 1.7, eggs laid on upper side of leaf, and laying eggs in groups. In addition, two other characters identified in this study support this relationship: larva with a pair of short dorsal fleshy humps on T1 (albeit *Forbestra olivencia*'s are shorter and more rounded than in *Mechanitis*), and in the pupa the dorsal abdominal spots lie near the dorsal midline.

The sister relationship of *Forbestra* and *Mechanitis* implies similarities in ecology and behavior between these genera. Observations on *F. olivencia* at Garza Cocha largely support this. For example, the single observation of *Mechanitis messenoides* using *F. olivencia*'s host suggests similar tolerances to host plant chemistry. Furthermore, *F. olivencia* feed on bird droppings and follow army ants similar to *Mechanitis* (Ray & Andrews 1980). Though the data are few (five females and one male were observed feeding on bird droppings), they show a female bias in feeding on bird droppings as documented for *Mechanitis* and *Melinaea* (Ray & Andrews 1980).

Males of ithomiine species avidly visit Asteraceae and Boraginaceae flowers and plant parts to gather pyrrolizidine alkaloids (Brown 1984a, 1984b, 1987, Brown et al. 1991, Pliske 1974, 1975). *Mechanitis* are commonly seen feeding on Asteraceae in gaps, secondary growth and cleared areas at Garza Cocha. Despite equal effort sampling all species of ithomiines and making observations in the early morning at flowers fed on by other ithomiine species, *F. olivencia* was not observed feeding on flowers during this study. This almost certainly does not reflect a difference between *F. olivencia* and *Mechanitis* and instead is attributed to chance. A male *Forbestra proceris* was found feeding on Asteraceae in an open habitat in the early morning. Furthermore A. Freitas has observed *F. olivencia* males visiting Asteraceae in the early morning in Brazil (pers. comm.).

There does seem to be a microhabitat difference related to host plant use between *F. olivencia* and *Mechanitis* species at this site. *F. olivencia* adults were not observed in open areas or in forest gaps. *Solanum monarchostemon* was found in and around gaps, and in well-lit areas of forest. *F. olivencia* eggs and larvae were not found on hosts in gaps or in sunny areas at gap edges. In contrast, *Mechanitis* eggs and larvae are commonly found on their host plants in gaps and open areas, and *Mechanitis* are more commonly seen flying in gaps and very open areas at this site. Differential microhabitat use by *F. olivencia* relative to *Mechanitis* deserves further investigation as it pertains to a correlation between microhabitat and mimicry (DeVries et al. 1999, Mallet & Gilbert 1995).

Despite the observation that specimens of *Forbestra* are uncommon in natural history collections (Fox 1967), *F. olivencia* was moderately common at Garza Cocha during this study ranking as the 13th most abundant

ithomiine. *F. olivencia* was highest in abundance in the drier months sampled (December to February) with 0.76 individuals per day in January-February 2003 and 0.62 individuals per day in December 2004 to January 2005. During the wetter months of May-August *F. olivencia* varied in abundance year to year (0.11, 0.23 and 0.47 individuals per day in 2000, 2001, 2002, mean = 0.27) but did not exhibit extreme fluctuations in abundance during the study period. Although all three *Forbestra* species have been observed at Garza Cocha they are not equal in abundance. *Forbestra olivencia* was much more common than both *F. equicola* and *F. proceris*. Ithomiines are numerically dominant members of neotropical mimetic butterfly assemblages (Beccaloni 1997, Brown & Benson 1974) and observations at Garza Cocha confirm this (unpublished). *F. olivencia* is likely an important component of the mimetic community at this site, being tied for the third most abundant ithomiine species of the 13 that share its mimetic color pattern.

Observations on parasitoids, predators and host abundance provide potential explanations for moderate population density of *F. olivencia* at this site and time period. Larval parasites were found in low abundance during rearing. Adults probably suffer mortality from avian predators as beak marks were found on the wings of some individuals. As mentioned above, ants in the genus *Crematogaster* attack eggs and are commonly seen patrolling the host plants. Thus, *Crematogaster* could play a role in population dynamics of *F. olivencia*. Given the careful searching by the female during oviposition it seems probable that females are checking for presence of ants, or assessing presence of conspecific eggs and larvae. The host of *F. olivencia* at Garza Cocha is not uncommon, but does not approach the high abundance of hosts of more common ithomiines at the site. Detailed study of these factors could contribute to the understanding of population dynamics in this species.

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APPENDIX: FIRST INSTAR CHAETOTAXY

In the description of first instar chaetotaxy that follows numbers in parentheses correspond to characters in Motta's (2003) Table 19.2. Setal nomenclature follows Motta (2003). Hinton (1946), Kitching (1984) and Peterson (1962) were also consulted. Descriptions are given here rather than a table of character states because of perceived ambiguity or difficulty interpreting some of the characters. In the following descriptions T1, 2, 3 are pro-, meso- and metathoracic segments respectively, A1-10 are abdominal segments, and unless otherwise noted setal characters apply to all segments where present.

Cephalic capsule. Seta C1 equidistant to frontal and anteclypeal sutures (1). Seta C2 nearer to C1 than to a medial imaginary line (2). Seta C2 same length at C1 (3). Seta F1 undoubtedly more dorsal and medial to C2 (4). Seta F1 nearer to C2 than it is to coronal bifurcation (5). Seta F2 equidistant or subtly nearer to frontal suture than to imaginary medial line (6). Puncture Fa clearly above seta F1 (7). Distance between Fa punctures similar to that between Fa and F1 (8). Puncture AFa, and setae AF1 and AF2 all present (9). Puncture AFa medial to line connecting setae AF1 and AF2, forming obtuse triangle with angle between AFa and AF1/AF2 ~160° (10). Puncture AFa closer to seta AF2 relative to AF1 (11). Setae AF1 and AF2 similar in length (12). Seta AF2 subtly above level of coronal suture bifurcation (13). Distance of seta AF2 to coronal suture same as distance of AF1 to frontal suture (14). Puncture Aa above line connecting AF1 and A2 (15). Puncture Aa nearer to A2 than to AF1 (16). Seta A3 just posterior to imaginary line between stemma iv and P1; distance of A3 to the imaginary line less than distance of A3 to stemma iv (17). Seta A1 closer to stemma i than ii and aligned to slightly above stemma i (18). Seta A2 aligned with imaginary line between stemma ii and AF1 (19). Seta A3 longer in length than A2 and L1 (20). Puncture Pa ventral to imaginary line connecting setae A2 and A3 (21). Puncture Pa nearer to seta A2 than to A3 (22). Puncture Pb medial to imaginary line between setae P1 and P2 (23). Puncture Pb closer to seta P2 than P1 (24). Seta P1 farther from coronal suture than is seta P2 (25). Seta P1 twice as long as length of P2 (26). Relative distance of puncture La to seta L1, 1/3 distance between L1 and A3 (27). Alignment of puncture La and setae L1 and A3 forming a triangle (28). Seta O1 nearly in line with i and iv, equidistant to iii and iv; distance of O1 farther to iii than ii (29). Angle formed between O2 and stemmata iv and v slightly less than 90° (30). Seta O2 equidistant to stemmata iv and v (31). Seta O2 longer than O1 and O3, with O1 and O3 similar lengths (32, 33). Seta O3 aligned to slightly ventral than stemma v and groove (34). Puncture Oa nearly aligned with stemma i and seta A1 and very near stemma i (35). Puncture Ob forming an angle between stemma v and O2 (36). Puncture Ob equidistant to v and O2 (37). SO1 in ventral end of antennal socket so that distance of SO1 to end of antennal socket is less than 1/2 distance between SO1 and SO3 (38). SO2 subtly ventral to stemmata v and vi (39). SO2 equidistant to v and vi (40). SO3 posterior to line between stemma vi and SO1 (41). SOa aligned to slightly nearer to suture relative to line between SO3 and G1 (42). SOa falls on line between SO2 and nearest point of maxillary (ventral) suture, SOa is closer to SO3 than to the suture and closer to the suture than to SO2 (43). SOb very near to the antennal socket (44). Relative distance of SOb to stemma vi and SO3 varies from nearer to stemma vi to equidistant (45). G1 closer to groove than to maxillary (ventral) suture (46). Ga ventral to line joining G1 and O3 (47). Ga slightly nearer to equidistant to G1 relative to O3 (48). V1 equidistant between P2 and "V" group (49). Stemmata all similar diameter (50). Distance from stemma iii to iv shorter than from i to ii, and ii to iii (51). Stemma v equidistant to iv and vi (52).

Mandible and labrum. Seta M2 aligned between L1 and L2 or aligned with L1 (53). Seta M2 subtly ventral to line between M1 and L2 (54). Seta M1 shifted dorsally relative to M2 (55). Distance between M1 setae equivalent to distance between M1 and M2 setae (56). Seta M2 about twice as long as M1 (57). Puncture S (called "S" in Motta 2003, called "P" in Peterson 1962) located nearer to the basal suture or posterior border relative to M1 and M2 (58, 61). Puncture S located dorsally and nearly in line vertically with M2 such that a line connecting the two would be nearly parallel to imaginary midline (59). Mean angle of lines connecting M1, M2 and puncture S 40 - 70° (60). Puncture S in line vertically with longest part of labrum (labral lobe) and very dorsal of widest part of labrum (between L1's) (62). Seta M3 on distal border of labrum (63). Seta L2 much nearer to L1 than to L3 (64). Seta L1 very slightly distal to widest part of labrum (65). Less sclerotized region of labrum spans notch to just before M3 (66). Less sclerotized basal patches absent (67). Internal border of labral lobe smoothly curved (68). Labral notch angle obtuse (69). Ratio of notch length (= depth) to overall labral length (labral lobe to base) ~ 0.8; ratio of notch width, as measured between M3's, to labral length ~ 0.8 (70). Ratio of labrum width (between L1's) to length (labral lobe to base) ~ 2 (71). More than three small molar teeth (72). Incisors 2 and 3 similar lengths (73). Lateral grooves radiating from each side of 4th incisor, 4 grooves in total (74).

Body. No tubercles present on the thorax (75). Average seta length is less than segment width except for the longer XD1 and XD2 setae on T1 which are nearly as long as segment width (77). Crochets arranged in a circle pattern (78) with inner and outer crochets similar length (79). Prolegs with more that 14 crochets on average (80). Cervical sclerite absent on XD1 and XD2 and D1 (81). Seta D1 shorter than XD1 and XD2 which are equivalent in length (82). Setae SD2 and SD1 aligned on T1, SD2 shifted slightly posterior to SD1 on T2 and T3, and SD2 shifted very posterior to SD1 on abdomen (83, 87). On segment T1 setae L1 and L2 slightly dorsal of spiracle with L2 between L1 and spiracle (84). Setae D1 and D2 are equivalent lengths (85, 91). Seta SD2 closer to SD1 on thorax but equidistant to SD1 and D2 on abdomen (86). Seta SD2 ventral and aligned with D1 and D2 on thorax but ventral and posterior to D1 and D2 on abdomen (88). Seta SD1 longer than L1 and equivalent to L2 on T1; SD1 equivalent to L1 and L2 on T2/3 and abdomen (89, 94). Seta L2 present on segments T1-A8 (90). Seta SD2 longer than D1 and D2 on T2/3, SD2 and D1/2 similar lengths on other segments (92). SD1 longer than SD2 on T1, SD1 slightly shorter than SD2 and equivalent to D1/2 on T2/3, and SD1 equivalent to slightly longer than SD2 on abdomen (93). Seta L2 longer than L1 on T1 and equivalent to slightly longer than L1 on other segments (95). Additional SV seta present only on T1 and A2 (96). Segment A9 relative to A7/8 missing two setae (one of L1/2 and one of SD1/2 (97). On segment A10 seta D1 longest, SD1 and L1 equivalent and D2 shortest (98). Setae P1 and SP1 both present on segment A10 (99).

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JOHN ABBOT'S "LOST" DRAWINGS FOR JOHN E. LE CONTE IN THE AMERICAN PHILOSOPHICAL SOCIETY LIBRARY, PHILADELPHIA

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ABSTRACT. Between 1813 and 1835, artist-naturalist John Abbot completed as many as 3,000 natural history illustrations for American naturalist John E. Le Conte. Long believed lost, the majority of these drawings are undoubtedly included among an extensive collection of small watercolors deposited in the American Philosophical Society Library. An overview of the collection is provided and several drawings of Lepidoptera are identified and figured. Le Conte's drawings of plants, reptiles, and amphibians are also discussed. Similar collections of drawings by Abbot are summarized.

Additional key words: Coleoptera, Georgia, John Lawrence LeConte, Lepidoptera

Introduction

Scudder (1884) observed that John Eatton Le Conte, Jr. (1784-1860) "left behind a most extensive series of water-color illustrations of our native insects and plants made with his own hands." He further described the insect drawings as small in size and "mounted on paper of variable form" (Scudder 1888-1889). He recognized that they were similar in format to other drawings once owned by the French entomologist Jean B. A. D. de Boisduval (1799-1879), who collaborated with Le Conte on a book about North American butterflies. Scudder used this as evidence to suggest that most of the illustrations in Boisduval & Le Conte (1829-[1837]) were derived from Le Conte, not John Abbot as generally accepted. Skinner (1911) later revealed that "the superb collection of Major LeConte's drawings of insects are now the property of the Missouri Botanical Garden."

Rehn (1954) described eight volumes of arthropod drawings that were acquired in 1953 by the American Philosophical Society, Philadelphia, Pennsylvania. Purchased from the Missouri Botanical Garden, they are some of the same drawings that were once owned by J. E. Le Conte. Rehn credited Le Conte as the primary artist, but speculated that "some of the illustrations in the volumes…may have been the work of John Abbot." However, he cautioned that there was "no definite evidence" to this effect, "other than information that Abbot supplied certain illustrations to J. E. Leconte." Rehn probably derived this information from Dow (1914a), who reproduced an 1835 letter in which Abbot estimated that Le Conte must have been in possession of "2 to 3000" of his drawings (transcript in Mayr Library, Harvard University). Abbot's friend, Augustus G. Oemler, noted in 1851 that "Major John Le Conte has a great number [of Abbot's drawings] but without the plants the insect feeds on" (letter to T. W. Harris, Mayr Library). Dow (1914b) speculated that Abbot's many drawings for Le Conte "probably still exist." "We can only wonder, with Dow," wrote Mallis (1971), "what happened to the some two or three thousand water colors of insects done by John Abbot, which the Major [J. E. Le Conte] had accumulated over many years."

Based mostly on Abbot's drawings and specimens, J. E. Le Conte co-authored a treatise on North American butterflies (Boisduval & Le Conte (1829-[1837]). It included the descriptions of many new species, but remained unfinished. A planned companion volume on moths was never attempted. Most of the original Abbot drawings that were used for the color plates in Boisduval & Le Conte (1829-[1837]) are deposited in the Thomas Cooper Library, University of South Carolina. Other Abbot drawings used for this book are missing and presumed lost (Calhoun 2004). These collections of illustrations were probably given to Boisduval by Le Conte, who visited Paris in 1828 (Sallé 1883). Le Conte retained other drawings by Abbot, adding to his collection until at least 1835. It is my contention that most of these remaining drawings have been improperly attributed to Le Conte for over a century. They likely played a crucial role in Le Conte's understanding of the invertebrate fauna of Georgia. Moreover, they possibly helped to encourage the entomological pursuits of his son, John Lawrence LeConte (1825-1883), who would become the most celebrated American entomologist of the 19th century. As another installment in my study of John Abbot's entomological contributions, I present a brief analysis of the illustrations at the American Philosophical Society Library and identify several Lepidoptera drawings that are believed to be the work of Abbot.

Methods

Drawings once owned by John E. Le Conte were examined and photographed at the American

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Philosophical Society Library and the Thomas Cooper Library (University of South Carolina). Le Conte's personal correspondence was also examined at the APS. Information on other Le Conte drawings was obtained from the Hesburgh Library (Notre Dame University). Relevant manuscripts and drawings were also consulted at The Natural History Museum, London, Linnean Society of London, Ernst Mayr Library (Museum of Comparative Zoology, Harvard University), and the Hargrett Rare Book and Manuscript Library (University of Georgia). Copies of additional manuscripts were obtained from the Carl A. Kroch Library (Cornell University).

RESULTS

Background. Artist-naturalist John Abbot (1751-ca.1840) first became acquainted with John E. Le Conte in 1813, when he mentioned "a Mr Le Compte who has a General taste for Nat. history," and further remarked that he was "Employed in Drawing the Georgian Insects for a Mr Le Compte, particularly the Coleoptera." That year, Le Conte engaged Abbot "to make a General Collection of & draw all the Coleoptera of Georgia for him, Then all the Lepidoptera." The following year, Abbot wrote, "I continue to draw for Mr Le Compte as leasure & opportunity permits." Abbot described his early relationship with Le Conte in more detail in 1816, explaining, "At present I am under no particular engagement to any person to collect or Draw for but only a Mr Le Conte…he has a Taste for General Natural history but seems mostly attached to Botany, for him I have Drawed and am continuing to Draw a large Collection of Insects. I believe he has some publication in view." Back to misspelling Le Conte's name in 1817, Abbot stated, "Mr Le Comte is not in the habit of keeping a collection of Insects, he only collects such as he wants me to draw for him" (letters to Heinrich Escher-Zollikofer, Kroch Library, and William Swainson, Linnean Society of London).

Le Conte's specimens probably explain the inclusion of the butterfly *Speyeria idalia* (Drury) among Abbot's drawings for Boisduval & Le Conte (1829-[1837]). This book gave the distribution of *S. idalia* as "environs de New-York et de Philadelphie" (environs of New York and Philadelphia), with no mention of Georgia. The erroneous mention of "Jamaique" (Jamaica) was probably derived from Cramer ([1775-1776]). Abbot previously illustrated this species, but from a male specimen collected by the South Carolina botanist Stephen Elliott who traveled northward in 1808. The reference to "New-York" may also have been derived from Cramer ([1775-1776]), but Le Conte lived in New York. Although the published plate was credited to Le Conte, it is more likely that the specimen came from him, not the original drawing (see Calhoun 2004).

Abbot eventually collected specimens for Le Conte, who requested in 1828 "an extensive Collection of Lepidopa & Coleoptera Insects" (Kroch Library). In 1835, Abbot was still corresponding with Le Conte, "for whom I continue to draw for every Year," though there is no evidence that he produced more drawings after 1835. Depending upon the size of the drawing, Le Conte paid Abbot from 6.25 cents ("16 for a Dollar") to 50 cents each (letter to T. W. Harris, Mayr Library).

In 1810, Le Conte's brother, Louis, assumed management of the family's rice plantation near Riceboro, Liberty County, Georgia. This immense plantation, called "Woodmanston," was located 40 km (25 mi) southwest of Savannah. A portion still remains as a botanical garden on the National Register of Historic Places (Armes 1903, Bigley 2001). John E. Le Conte often traveled to the plantation during the winter months. Abbot may even have visited Le Conte at Woodmanston (Bigley 2001).

After the death of J. E. Le Conte, his collection of drawings passed into the hands of his son, famed coleopterist John Lawrence LeConte (1825-1883), whose own library was sold in 1884 (Henkels 1884, Scudder 1888-1889). Although his father signed his name as "Le Conte" (Calhoun 2005), signatures of John Lawrence indicate that he preferred the compressed variant of "LeConte." Both of these versions have repeatedly been simplified in the literature – even during their lifetimes – to read "Leconte." The altered spellings of J. E. Le Conte's name by Abbot are not surprising, as Abbot often varied correspondent's names (Calhoun in press). Interestingly, his spellings of "Le Compte" and "Le Comte" are also known variants of this French surname. All these variations have contributed to the persistent confusion over the proper format of this name. It is therefore advisable to abide by the signatures of the naturalists themselves.

At the time of J. L. LeConte's death in 1883, he possessed 4,765 original drawings of arthropods, reptiles, amphibians, and flowers. They were contained in twelve portfolios that Henkels (1884) described as "Scrap-books, filled with Figures of Entomological Specimens, faithfully drawn and artistically colored by hand, by the late Major [J. E.] and Dr. [J. L.] Le Conte." The arthropod drawings were purchased at the J. L. LeConte library auction by the Pennsylvania botanist Benjamin M. Everhart (1818-1904). After the death of Everhart, they were acquired by the naturalist Samuel N. Rhoads, who owned the Franklin Book Shop in Philadelphia. According to a letter dated 8 December 1905, Rhoads unsuccessfully offered them to the

philanthropist Wymberly Jones De Renne (1853-1926) of Wormsloe, Georgia. Under the heading "Quotation on 8 Leconte Portfolios," Rhoads described them as "the original handiwork of Major Dr. Leconte…Most of them are on single sheets 5 x 3 inches and were evidently intended for an extensive illustrated monograph never published." He noted that they "came from the B. M. Everhart collection recently sold, he having purchased them at the sale of Le Conte's effects in this city many years ago" (Hargrett Library). Rhodes seems to have combined father and son into a single person by his reference to "Major [John Eatton] Dr. [John Lawrence] Leconte." In 1907, Rhoads sold the drawings to the Missouri Botanical Garden. Inscribed in pencil on the 1905 letter to De Renne is a signed memorandum by Rhoads, dated 1918, that reads, "Mr. De Renne did not buy these. They were sold to the St. Louis Botanical Garden." Rhoads must have been visiting W. J. De Renne when he inserted this annotation. The Missouri Botanical Garden sold these drawings in 1953 to the American Philosophical Society. The published library catalog of the American Philosophical Society ([APS 1970]) listed letters and other materials pertaining to the provenance of these drawings, but repeated attempts by current librarians to locate them were unsuccessful.

The 49 drawings of reptiles and amphibians by J. E. Le Conte are now deposited in the Hargrett Rare Book and Manuscript Library, University of Georgia. They were evidently purchased by B. M. Everhart at the J. L. LeConte library auction. After Everhart's death, they were obtained by S. N. Rhoads, probably in 1905, who shortly after sold them to W. J. De Renne. Inscribed on a flyleaf of this volume is a notation by De Renne that reads, "bought from S. N. Rhoads, Phila. Nov. 27, 1905" (Mary Ellen Brooks pers comm.). These drawings were purchased less than two weeks before Rhoads offered the arthropod drawings to De Renne. They were listed in the 1931 De Renne Library catalog as "Forty-Nine original Drawings in Color, by Leconte, of the Turtles, Tortoises, Frogs and Salamanders of Georgia and South Carolina" (Mackall 1931). The collections of the De Renne Library were acquired in 1938 by the University of Georgia.

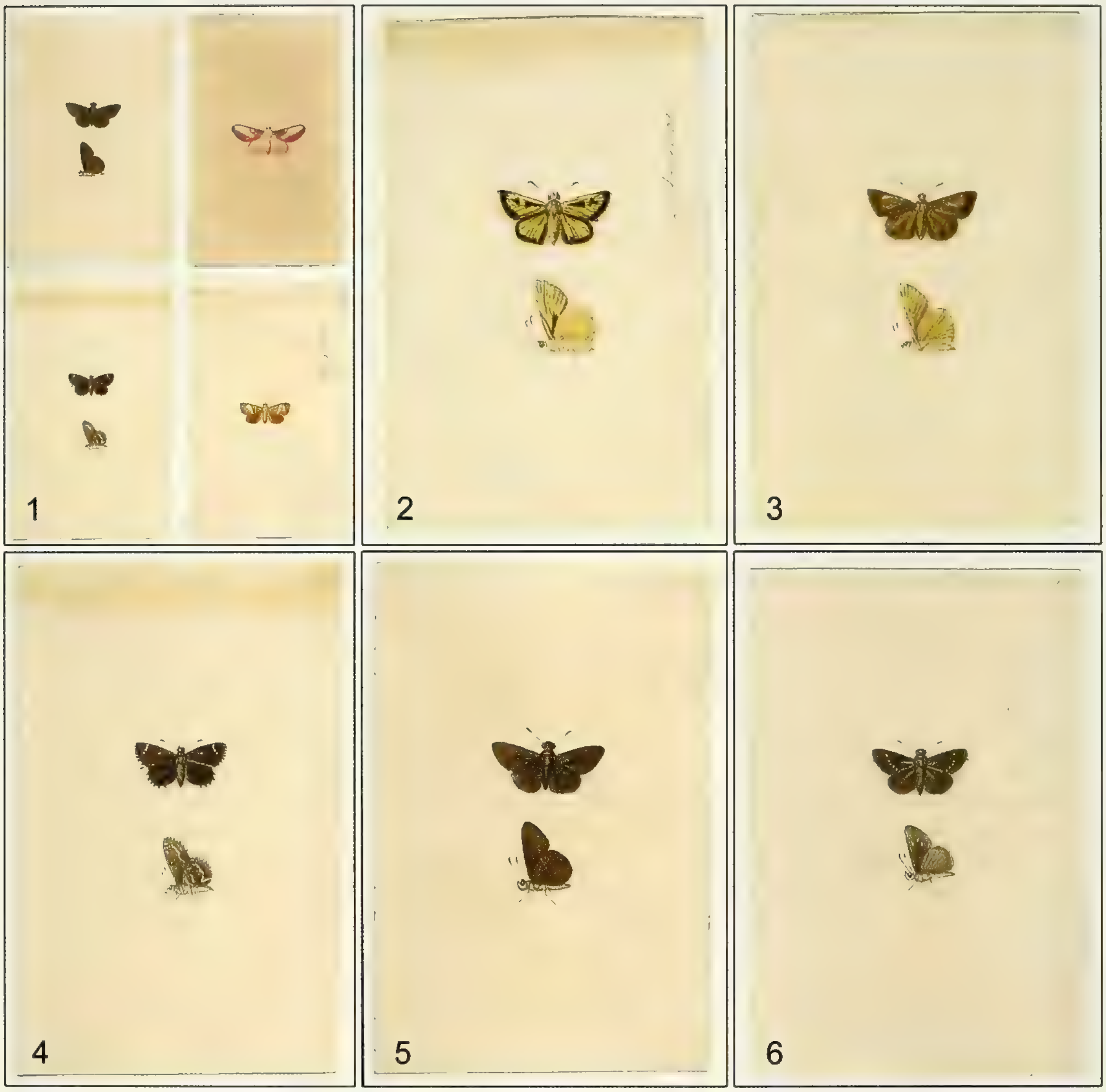
The 42 flower illustrations by J. E. Le Conte are preserved in the Hesburgh Library, University of Notre Dame. A manuscript note pasted on the inside front cover of this volume indicates that they were purchased at the J. L. LeConte library auction by the New Jersey botanist Isaac C. Martindale (1842-1893). After the death of Martindale, these drawings were presumed lost. In 1897, the botanist Edward L. Greene (1843-1915) stumbled upon them in a secondhand bookstore in Philadelphia. Either as a gift from Greene, or upon his death, they were acquired in 1915 by the University of Notre Dame (Baird 1938, Nieuwland 1917).

Illustrations from these portfolios were used for the published descriptions of several new species, most notably in the botanical works of Le Conte (1824a, 1824b, 1828). Le Conte did not reproduce his flower drawings, but they were later figured by Nieuwland (1917). As suggested by Rehn (1954), some of the insect drawings may portray type specimens, but additional research is necessary to determine if any were reproduced to accompany published descriptions. None of them appeared in Boisduval & Le Conte (1829-[1837]).

Analysis. The American Philosophical Society acquired eight volumes of arthropod drawings, bound with board covers and leather spines (Rehn 1954). This corresponds to the earlier description by bookseller S. N. Rhoads; "Eight large 4to portfolio Scrap Books bound in $^1/_2$ morocco" (1905 letter to W. J. De Renne, Hargrett Library). Although Henkels (1884) previously listed ten volumes of arthropod drawings, each portfolio was sold as a separate lot at the 1884 J. L. LeConte library auction. The two additional portfolios were presumably not purchased by B. M. Everhart.

The remaining eight portfolios of arthropod drawings were re-housed in 1987 and placed into beige buckram cases with gilt titles that read "LECONTE/ENTOMOLOGICAL DRAWINGS." They comprise over 3,700 small drawings, which typically include only one or two figures each (Fig. 1). From two to nine drawings are pasted onto larger sheets of paper measuring 21.6 x 35.6 cm (8.5 x 14.0 in). Individual pages are now enclosed within clear archival sleeves. Written in graphite in the first volume is the title, "Portfolio of Original Figures of Entomological and Other Subjects by Le Conte." This title page was possibly created in 1884 for the J. L. LeConte library auction. Stamped in red ink at the bottom of the page is "Mo. Bot. Garden/1907." Also written at the beginning of the first volume is "Am. Philosophical Soc./Dec. 15, 1953/Philadelphia."

It is reasonable to assume that J. E. Le Conte and his son were responsible for initially arranging and mounting the drawings. Most possess handwritten numbers, which are not consecutive and were obviously added before the drawings were pasted onto the larger sheets of paper. Many also bear scale lines that indicate the actual sizes of the depicted subjects, which were sometimes drawn larger to show more detail. Inscriptions in Abbot's hand, including penciled numbers, are present on some of the drawings. A few are signed and dated by the naturalist Titian R. Peale



FIGS. 1-6. Drawings probably by John Abbot in the American Philosophical Society Library. 1, four drawings of butterflies (left) and moths on a page in the second volume. The moths are *Dryocampa rubicunda* (Fabricius) (top right) and probably *Lithacodes fasciola* (bottom right). 2, female *Anatrytone logan* (graphite "Hesperiidae" in an unknown hand). 3, female *Atrytone arogos*. 4, female *Amblyscirtes* sp., possibly *alternata*. 5, male *Euphyes vestris*. 6, probably a female *Euphyes vestris*.

(1799-1885). Some give localities such as "Texas" and "Europe," suggesting they were probably drawn and inscribed by J. L. LeConte and possibly also his father. The majority of the insect drawings portray Coleoptera. Others depict species of Diptera, Hemiptera, Hymenoptera, and Lepidoptera. In addition to insects, there are spiders and a few species of myripods. Rehn (1954) discussed additional details about the volumes.

The Lepidoptera are contained in the second volume, with 85 drawings of over 200 figures rendered on cream colored wove paper. The overall quality of these drawings is good, but some are decidedly inferior. All but five portray moths, mostly diminutive species. The remaining five drawings, measuring approximately 14.6 x 11.4 cm (5.8 x 4.5 in), are butterflies of the family Hesperiidae. They are included on the first three pages of the volume and each depicts life-sized dorsal and ventral aspects of a single species. I have identified them as: no. 15, female *Anatrytone logan* (W. H. Edwards) (Fig. 2); no. 16, female *Atrytone arogos* (Boisduval & Le Conte) (Fig. 3); no. 17, female *Amblyscirtes* sp. (Fig. 4); no 43, male *Euphyes vestris* (Boisduval) (Fig. 5); no. 44, probably a female *Euphyes vestris* (Fig. 6). The figures on drawing no. 17 are poorly rendered, but may be exaggerated representations of *Amblyscirtes alternata* Grote &

Robinson, which John Abbot illustrated several times. The identity of no. 44 is indeterminate, but its consecutive number suggests that it was intended to portray the female of no. 43.

Despite the conclusion by Rogers-Price (1983, 1997) that some of the drawings in these eight volumes are the work of Abbot, most continue to be credited to J. E. Le Conte. However, Abbot stated that most of his illustrations for Le Conte were small in size. Abbot wrote in 1833, "as to the number of Paintings I have made either for F^n [Francillon] or Le Conte…I made about 350 Q^o [quarto] of the changes of the Insects for Mr F^n & 2000 small ones, & 500 Spiders, & must have made more small ones than that for Le Conte" (letter to A. G. Oemler, Mayr Library). Abbot further remarked in 1835 that "Mr Le Conte preferred a single Insect on a paper, as he said he cou'd then class them as he received them." He noted that these drawings depicted "mostly small Insects, & many are Minutia." He drew "magnified" (enlarged) figures of the smallest species so that they would "shew better" (letter to T. W. Harris, Mayr Library).

Abbot executed numerous small illustrations during his long career in America. Many drawings for London jeweler John Francillon (1744-1816) were purchased in 1818 by The Natural History Museum, London. They include watercolors that are reminiscent of those at the American Philosophical Society, with single insects and spiders portrayed on small pieces of paper. Enlarged figures of very small species are likewise accompanied by outlines or scale lines that indicate the actual sizes of the subjects. Two other volumes of small drawings of moths were acquired by The Natural History Museum in 1910 as part of the bequest of Thomas de Grey, 6th Baron Walsingham. Gilbert (1998) questioned their association with Abbot, but they are consistent with his work and portray species that occur in Georgia. These drawings were probably from among the "2000 small ones" that Abbot completed for Francillon.

Abbot also sent numerous small drawings to English naturalist William Swainson (1789-1855). Abbot described these in 1835 as "about 650 Drawings of single Insects, on small papers" (Parkinson 1978). The Alexander Turnbull Library (Wellington, New Zealand) preserves a series of 27 small watercolors of moths that were acquired in 1927, rendered on papers as tiny as 9.3 x 9.2 cm (3.7 x 3.6 in). They lack inscriptions, but the format and artistic style are like the small drawings in London and the American Philosophical Society. They even possess the same type of scale lines. The species portrayed in these drawings are found in Georgia, confirming their likely origin with Abbot (Calhoun in press). Swainson moved from London to New Zealand in 1840. The remainder of the 650 small drawings may have been lost in September 1841 when a ship carrying a portion of Swainson's library sunk en route to his new home.

French naturalist Jean B. A. D. de Boisduval possessed a large number of small drawings that Scudder (1888-1889) examined during a trip to Paris, probably in 1871. Some were purchased at auction in 1964 by the University of South Carolina. Although several are probably by J. E. Le Conte, others are consistent with Abbot's style and even include inscriptions in his hand (Calhoun 2004). Boisduval possessed 452 other small drawings of Lepidoptera, measuring 13.0 x 8.5 cm (5.0 x 3.3 in). Oberthür (1920) attributed them to Le Conte, but they were more likely from Le Conte's collection of Abbot drawings. Contained in two bound volumes, they were auctioned to a London firm in 1963 (Sotheby & Co. 1963, Cowan 1969) and their disposition is unknown. The Sotheby auction catalog credited them to John L. LeConte.

Discussion

Evidence strongly suggests that the majority of the drawings at the American Philosophical Society are by Abbot and they represent the bulk of the enigmatic "2 to 3000" drawings that he completed for J. E. Le Conte between 1813 and 1835. They agree with Abbot's own description of these illustrations and their format is like his other small watercolors. In addition, many figures of Lepidoptera are duplicated in other sets of Abbot's drawings. This includes a unique interpretation of what is thought to be the moth *Lithacodes fasciola* (Herrich-Schäffer) (Fig. 1, bottom right). I have found duplicates of this figure among Abbot's drawings at the Thomas Cooper Library and the Alexander Turnbull Library.

Following Rehn (1954), I previously attributed several Lepidoptera drawings in the American Philosophical Society to J. E. Le Conte (Calhoun 2003). Despite their poor quality, they were undoubtedly rendered by Abbot. Entomologists are generally familiar only with Abbot's larger and more elaborate life history compositions that include hostplants, like those published in Smith & Abbot (1797) (see Calhoun 2006). Three sets of these life history drawings, probably also owned by J. E. Le Conte, were used to create some of the color plates in Boisduval & Le Conte (1829-[1837]) (Calhoun 2004). These illustrations, missing and presumed lost, were probably completed ca. 1810-1815. After his arrival in America, Abbot composed insect drawings in four principal layouts: 1) designs that incorporated one or more species and a supposed hostplant, or a plant inserted for decorative purposes, 2) adults and early stages of one or more species, grouped

in a linear format, 3) geometric designs of adults of multiple species, and 4) one or two figures of adults and/or early stages on small pieces of paper. This flexibility allowed Abbot to sell more of his drawings.

Abbot's relationship with Le Conte was coming to close by 1836 when he lamented, "I have no correspondents (Naturalists) at present but Mr Oemler & Mr Le Conte & I don't hear from them often" (letter to H. Escher-Zollikofer, Kroch Library). Unfortunately, their long association was strained and ultimately ended badly. Abbot stated in 1814 that the low price that Le Conte paid for his drawings would "not admit me to make it my sole employment" (Kroch Library). In 1851, many years after Abbot's death, Augustus G. Oemler defended Abbot to Thaddeus W. Harris, arguing, "Le Conte brags a good deal that he "maintained Abbot for several years." How did he do it? He allowed him for each insect, large or small, in nature and a correct portrait of it, the enormous sum of Six and a quarter Cents, and after all, disputing the last bill of the old man, thus cheating him" (Mayr Library).

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THE DIANA FRITILLARY (*SPEYERIA DIANA*) AND GREAT SPANGLED FRITILLARY (*S. CYBELE*): DEPENDENCE ON FIRE IN THE OUACHITA MOUNTAINS OF ARKANSAS

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ABSTRACT. The Diana fritillary (*Speyeria diana*), a species of conservation concern throughout its range, and the great spangled fritillary (*S. cybele*) both occur in the Ouachita Mountains of west-central Arkansas and eastern Oklahoma. Both species depend on abundant, high quality nectar resources to support populations. Decades of intense fire suppression have greatly altered vegetation structure throughout the Ouachita Mountains resulting in profound ecological changes. In an effort to restore pre-European ecological relationships and biodiversity, managers are restoring shortleaf pine-bluestem communities with the use of frequent prescribed fire. Restored sites support greater abundances of nectar resources and *Speyeria diana* and *S. cybele* than fire suppressed controls.

Additional key words: Interior Highlands, surveys, restoration

INTRODUCTION

The Diana fritillary, *Speyeria diana* (Cramer) is a species of conservation concern throughout its range in the eastern United States. It is currently restricted to the Interior Highlands of Arkansas, Oklahoma, and possibly Missouri, and the Appalachian Mountains from the Virginias to Georgia and Alabama (Hovanitz 1963, Opler & Krizek 1984, Carleton and Nobles 1996, Moran and Baldridge 2002). Historical populations in the Midwest and the Virginia Piedmont were extirpated in the 1800s (but see Shull 1987) and the 1950s (Opler and Krizek 1984), respectively. The cause(s) of these range contractions is unknown; but habitat alteration including loss of forest habitat (Allen 1997), harvest of old-growth forests (Hammond and McCorkle 1983), and loss of nectar plants (Moran and Baldridge 2002) have been proposed.

In the Interior Highlands, Carleton and Nobles (1996) reported records of *S. diana* from 11 counties in Arkansas, Missouri, and Oklahoma since 1980 and an additional 10 counties prior to 1980. Moran and Baldridge (2002) reported recent records for an additional seven counties in Arkansas, and our records add an additional three counties (reported in Moran and Baldridge 2002). Based on these records, *S. diana* remains widespread in the Ouachita Mountains of Arkansas and Oklahoma and perhaps less so in the Ozark Mountains of Arkansas and Missouri.

The great spangled fritillary, *S. cybele* (Fabricius), is widespread in the eastern United States and Canada (Opler and Krizek 1984). It remains relatively common in a variety of habitats throughout most of its extensive range and is common throughout the Ouachita Mountains of Arkansas.

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The Ouachita Mountains physiographic region encompasses an area of 3,237,600 ha of east-west oriented ridges and valleys with elevations ranging from 150 to 820 m (Bukenhofer and Hedrick 1997). Historically, much of the region (especially the more xeric south- and west-facing slopes) burned on a regular basis during fires ignited by lightning and Native Americans (Foti and Glenn 1991, Masters *et al*. 1995). These frequently burned forests consisted of open, pine-dominated canopies, sparse midstories, and a diverse understory of grasses and forbs (Featherstonhaugh 1884, du Pratz 1975, Nuttall 1980, Foti and Glenn 1991, Masters *et al*. 1995). In the absence of frequent fire, these forests tend to succeed to an oak (*Quercus* spp.)-hickory (*Carya* spp.) community (Neal and Montague 1991).

Managers of the Ouachita National Forest have been in the process, since 1979, of restoring the fire-maintained shortleaf pine (*Pinus echinata* P. Mill.)-bluestem grass (*Schizachrium* spp.) ecosystem on approximately 48,706 ha primarily on the Poteau Ranger District in west-central Arkansas (Bukenhofer and Hedrick 1997). The primary management tool used to restore shortleaf pine-bluestem habitat is prescribed fire. Restoration is being conducted to restore habitat for the federally endangered red-cockaded woodpecker, *Picoides borealis* (Viellot), and to restore what is thought to be the original forest structure (Foti and Glenn 1991, Bukenhofer and Hedrick1997). A number of authors have examined the effect of these restoration efforts on a variety of taxa (Masters *et al*. 1998, 2002; Sparks *et al*. 1998, 1999; Thill *et al*. 2004).

As part of extensive studies on the effects of restoration of fire-maintained pine-bluestem habitats on lepidopteran communities, we conducted censuses of butterflies and nectar resources on restored (treatment)

and unrestored (control) plots (Thill *et al.* 2004). Here we report results for *S. diana* and *S. cybele* and their nectar resources in relation to ecosystem restoration and the prescribed fire regime.

STUDY AREA AND METHODS

This research was conducted on the Poteau District (34°45'N, 94°15'W) of the Ouachita National Forest in west-central Arkansas. The Ouachita Mountains, especially within the Ouachita National Forest, is predominately forested. North-facing slopes are dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and a diverse array of additional species, south-facing slopes by shortleaf pine and a varying mixture of angiosperms.

Landscape scale restoration was initiated in 1979, formally incorporated into the Ouachita National Forest Plan in 1996, and currently projects the restoration of 48,706 ha (7.3% of the Forest) to a shortleaf pine-bluestem condition thought to mimic the pre-European forest structure (U. S. Forest Service 1996, Bukenhofer and Hedrick 1997). At the initiation of our studies, approximately 9,071 ha had been restored in a 42,148 ha landscape on the Poteau Ranger District (W. G. Montague pers. com.). Restoration was accomplished by selective thinning of overstory trees, removal of most midstory vegetation, and implementation of a three-year prescribed fire regime. Treatment blocks for restoration are typically 10-45 ha in size, however blocks are combined for purposes of prescribed burning, and individual prescribed fires ranged up to 1,300 ha. We use "restored" in a relative sense and recognize that stands are on a trajectory towards an ecological state thought to mimic pre-European conditions.

We established nine study plots in restored stands and three in control stands. All restored stands had received initial thinning harvests and a minimum of four prescribed fires prior to the initiation of this study. Prescribed fire was applied to restored stands during March and April with few exceptions, all prior to the initiation of this study. During the course of this study prescribed fire was applied to three of the restored stands each year. Consequently, in any given year three restored stands represented first, second, and third growing seasons post-fire. For purposes of analysis, data were grouped by post-fire growing season.

Adult butterflies (Papilionoidea and Hesperioidea) were censused using a time-constrained walking census along a 500-m transect traversing a triangular course within each of the 12 study sites (Pollard 1977, Gall 1985). Individual transects were censused by slowly walking the length of the transect in approximately 20 min. Time required to count butterfly aggregations, net and identify individuals, and pauses to wait for appropriate wind or sun conditions (see below) was not included in the 20-min census time. All butterflies detected along the census transect during the 20-min census period were counted, regardless of distance from the midline of the transect. Consequently, comparisons across species, especially for species of different sizes or behaviors, are not appropriate. Most individuals (87.2%) were identified to species.

Census counts were conducted four times per year (first week of April, June, August, and October) during 2000 to 2002. Census counts on each site were replicated three times (a different observer on three separate days) during each month surveys were conducted. Individual censuses were conducted between 0900 and 1330 hrs CST on days when temperatures were between 18° and 36° C and wind velocity beneath the canopy was not strong enough to suppress butterfly flight (Beaufort Scale < 4). Census counts were further restricted to periods when sunlight was sufficient to cast discernable shadows. The response of butterflies to temperature, wind, and cloud cover varies seasonally and daily in complex ways. Consequently, observer judgment further constrained censusing to those periods when butterfly flight activity was judged to be substantial.

Nectar resources were quantified during each butterfly sampling month within three 1- x 100-m belt transects located parallel to each butterfly census transect. All nectar resources were counted and recorded by species. For most species, individual flowers or composite heads (capitula) were enumerated. Inflorescenses, or portions thereof, were counted for a few species with small and/or dense aggregations of flowers (e.g. *Ceanothus americanus* L., *Allium* sp., *Solidago* spp., Apiaceae). Enumeration decisions were based on the structure that most closely approximated a separate landing site for a typical butterfly.

In addition, throughout our investigations (1999-2004) in the Ouachita Mountains, we recorded observations of nectaring and other feeding activities. Date, resource, and butterfly species were recorded. Voucher specimens of plant species were collected for later identification. Plant nomenclature follows Smith (1994). Plant vouchers will be deposited in the Stephen F. Austin State University Herbarium, Nacogdoches, TX.

RESULTS

In the Ouachita Mountains, male *S. diana* emerge in late May to early June and *S. cybele* emerge in mid- to late May. Females of both species emerge approximately 7-10 days later in each species. Adult

males are generally dead by early July, although very worn males are occasionally noted as late as early October. Females are less obvious until late September-early October when numerous individuals, still in fairly good condition, are frequently observed.

Nectaring observations for *S. diana* (n = 307) and *S. cybele* (n = 607) were obtained during 1999-2004 (Table 1). Both species used a small subset of the total nectar species available and used by the total butterfly fauna throughout the flight period. More than 95% of *S. diana* nectaring records were from only eight plant species and more than 88% of *S. cybele* records were from only 11 species. Nectaring by *S. diana* was recorded on 11 additional species and by *S. cybele* on 26 additional species. These numbers were summed over the entire flight period, however the pattern was even more extreme within individual months. All but one of the heavily used species (*Carduus nutans* L.) and most of the rarely used species were native, herbaceous perennials. *Allium canadense* L. was the only monocot used by both species.

The availability and use of nectar resources varied considerably across months (Table 1). During the main flight period of males of both *Speyeria* species (late May and June), the primary nectar resources used were *Asclepias tuberosa* L., *Monarda fistulosa* Sims, *Cirsium carolinianum* (Walt.) Fern. & Schub., *Echinacea purpurea* (L.), *E. pallida* (Nutt.), and *Pycnanthemum tenuifolium* Schrad. Male *S. cybele* also used *Carduus nutans* and *Liatris squarrosa* (L.) Michx. Females tended to use the same species during this period. However, due to the slightly later emergence of females, the rapidly declining availability of *A. tuberosa*, *Cirsium carolinianum* and *E. pallida* flowers early in June reduced use of these species by females, especially the later emerging *S. diana*. Nectaring records were infrequent during July and August; as most males were dead and females were infrequently observed. *Pycnanthemum albescens* Torr. & Gray dominated the few nectaring records of both species during this period. Females became much more obvious during September and October and nectaring was primarily on *Cirsium discolor* (Muhl. ex. Wild.) Spreng.

Males of *S. diana* were frequently (n = 118) observed imbibing from non-nectar, apparently electrolyte rich resources (Smedley and Eisner 1995) including feces of a wide variety of vertebrates, carrion, wads of grass vomitus from coyotes, human sweat, damp soil, and dusty surfaces (i.e. roads, vehicles, etc.)(Table 1). This behavior was observed exclusively in newly eclosed males, possibly during their first two days, as judged by fresh appearance and absence in previous days. This behavior was less frequently (n = 67) observed in *S. cybele*, presumably because our June survey period was several days after most males of the earlier emerging *S. cybele* had discontinued this ephemeral behavior.

A consequence of the above behavior for male *S. diana*, and presumably for the earlier emerging *S. cybele*, was frequent vehicle-related mortality. Imbibing from feces, carrion, etc. was most frequent in the morning shortly after individuals first began flying, and occurred most frequently on unpaved roads where feces and carrion were common. Aggregations of up to 16 male *S. diana* were often present at a single site and they were generally reluctant to take flight. Consequently, multiple mortalities were not uncommon.

A total of 73 *S. diana* and 201 *S. cybele* were detected during a total of 324 census transects during 2000, 2001, and 2002 (Table 2). Equal numbers of transects (n = 36) were conducted in early June, early August, and early October of each year. Most detections were during the June surveys immediately following emergence of adults, with reduced numbers, primarily females, in August and October. Significant differences across treatments were detected for total numbers of both *S. diana* (χ^2 = 39.6, df = 3, P <0.001) and *S. cybele* (χ^2 = 166.6, df = 3, P <0.001). The overwhelming majority of detections of *S. diana* (71 of 73, 97.3%) and *S. cybele* (197 of 201, 98.0%) were from the restored treatments. Among the restored treatments, abundances for both species were highest during the second growing season post-fire.

A broadly similar pattern existed for the nectar resources (Table 3). With minor exceptions, nectar resources were more abundant in restored treatments than in controls, and more abundant during growing seasons most proximal to prescribed fires. Significant differences existed for many of these patterns. In most comparisons, significantly more nectar resources were detected in 1st and 2nd years post-burn than in the corresponding controls. Exceptions were the April 1st year post-burn sites in 2000 and 2001 when plants had not had sufficient time to recover from the very recent prescribed fires, and the 1st year post-burn sites in April 2002 when prescribed-burning was delayed until after the scheduled surveys. The only other exception was the 2nd year post-burn sites for April 2002. The prescribed fires during 2001 in each of the three replicates for this treatment were unusually intense, with substantial canopy mortality. The recovery rate of herbaceous plants was tremendous, and the anomalously low counts of nectar resources in April 2002 may have been a result of shading by the very high residual herbaceous biomass remaining from the 2001 growing season.

TABLE 1. Feeding records (1999-2005) of Diana fritillary (*Speyeria diana*) male/female and great spangled fritillary (*Speyeria cybele*) male/female/unknown in the Ouachita Mountains of western Arkansas by month.

Source	Species	May	Jun.	Jul.	Aug.	Sept.	Oct.	Total
Major Nectar Species								
Asclepias tuberosa L.	*S. diana*	0	18/0	0	0	0	0	18
	S. cybele	0/0/1	41/25/56	0	0	0	0	123
Echinacea purpurea (L.)	*S. diana*	0	11/2	0/1	0	0	0	14
	S. cybele	0	6/14/4	0/0/8	0	0	0	32
Echinacea pallida Nutt.	*S. diana*	3/0	0	0	0	0	0	3
	S. cybele	0/0/9	0/0/8	0	0	0	0	17
Cirsium carolinianum (Walt.)	*S. diana*	0	23/1	0	0	0	0	24
Fern. & Schub.	*S. cybele*	0/0/9	21/23/31	0	0	0	0	83
Cirsium discolor (Muhl.)	*S. diana*	0	0	0	0	1/147	0/23	171
Spreng.	*S. cybele*	0	0	0	3	0/43/24	0/0/12	82
Carduus nutans L.	*S. diana*	0	0	0	0	0	0	0
	S. cybele	0/0/11	0/0/9	0	0	0	0	20
Liatris elegans (Walt.) Michx.	*S. diana*	0	0	0	0	0	0/11	11
	S. cybele	0	0	0	0	0	0/5/0	5
Liatris squarrosa (L.) Michx.	*S. diana*	0	0	0	0	0	0	0
	S. cybele	0	2/4/20	0	0	0	0	26
Monarda fistulosa L.	*S. diana*	0	21/13	0	0	0	0	34
	S. cybele	0	9/11/93	0/0/5	0	0	0	118
Porteranthus stipulatus (Muhl.)	*S. diana*	0	1/0	0	0	0	0	1
Baill.	*S. cybele*	0	0/0/18	0	0	0	0	18
Pycnanthemum albescens Torr.	*S. diana*	0	0	0	0/8	0	0	8
& Gray	*S. cybele*	0	0	0	0/8/2	0	0	10
Pycnanthemum tenuifolium	*S. diana*	0	5/7	0	0	0	0	12
Schrad.	*S. cybele*	0	1/2/6	0/0/5	0	0	0	14
Secondary Nectar Species								
Cephalanthus occidentalis L.	*S. cybele*	0/0/4	0	0	0	0	0	4
Rhexia sp.	*S. diana*	0	0	0	0/1	0	0	1
Scutellaria ovata Hill	*S. diana*	0	1/0	0	0	0	0	1
	S. cybele	0	0/0/1	0	0	0	0	1
Erigeron strigosus Willd.	*S. diana*	0	1/1	0	0	0	0	2
	S. cybele	0	1/0/1	0	0	0	0	2
Bidens aristosa (Michx.) Britt.	*S. diana*	0	0	0	0	0/1	0	1
Eupatorium fistulosum Barr.	*S. diana*	0	0	0	0/1	0	0	1
Solidago rugosa (Small) Fern.	*S. diana*	0	0	0	0	0	0/1	1
Helianthus divaricatus L.	*S. diana*	0	1/0	0	0	0	0	1
	S. cybele	0	0/0/2	0/0/2	1/0/0	0	0	5
Vernonia gigantea (Watt.) Trel.	*S. diana*	0	0	0	0	0/1	0	1
	S. cybele	0	0	0	0	0/1/0	0/1/0	2
Vernonia baldwinii Torr.	*S. diana*	0	2/0	0	0	0	0	2
	S. cybele	0	0	0/0/1	0/0/2	0	0	3

(continued)

TABLE 1. (continued)

Source	Species	May	Jun.	Jul.	Aug.	Sep.	Oct.	Total
Achillea millefolium L.	*S. cybele*	1/0/0	0	0	0	0	0	1
Coreopsis palmata Nutt.	*S. cybele*	0/0/1	0	0	0	0	0	1
Coreopsis grandiflora Sweet	*S. cybele*	0	0/0/2	0	0	0	0	2
Coreopsis tripteris L.	*S. cybele*	0	0	0/0/1	0	0	0	1
Rudbeckia hirta L.	*S. cybele*	0	0/0/2	0	0	0	0	2
Verbesina helianthoides Michx.	*S. cybele*	0	2/0/7	0/0/3	0	0	0	12
Silphium integrifolium Michx.	*S. cybele*	0	0	0/0/1	0	0	0	1
Parthenium integrifolium L.	*S. cybele*	0	0/0/2	0	0	0	0	2
Aster ericoides L.	*S. cybele*	1/0/0	0	0	0	0	0	1
Trifolium pratense L.	*S. cybele*	1/0/0	1/0/0	0	0	0	0	2
Cornus drummondii C. A. Mey.	*S. cybele*	0	0/0/2	0	0	0	0	2
Daucus carota L.	*S. cybele*	0	0/0/1	0	0	0	0	1
Phlox glaberrima L.	*S. cybele*	0	0/0/1	0	0	0	0	1
Prunella vulgaris L.	*S. cybele*	0/0/1	0	0	0	0	0	1
Strophostyles leiosperma (Torr. & Gray) Piper	*S. cybele*	0	0	0	0/0/2	0	0	2
Aralia spinosa L.	*S. cybele*	0	0	0	0/0/2	0	0	2
Lonicera japonica Thunb.	*S. cybele*	0	2	0	0	0	0	2
Ligustrum vulgare L.	*S. cybele*	0/0/2	0	0	0	0	0	2
Ruellia sp.	*S. cybele*	0	0/0/1	0	0	0	0	1
Allium canadense L.	*S. cybele*	0/0/4	0	0	0	0	0	4
Carrion	*S. diana*	0	5/0	0	0	0	0	5
	S. cybele	5/0/0	1/0/0	0	0	0	0	6
Feces	*S. diana*	0	83/0	0	0	0	0	83
	S. cybele	36/0/01	18/0/0	0	0	0	0	54
Vomitus[1]	*S. diana*	0	5/0	0	0	0	0	5
Sweat (human)	*S. diana*	0	5/0	0	0	0	0	5
Wet Soil	*S. diana*	0	18/0	0	0	0	0	18
	S. cybele	0	7/0/0	0	0	0	0	7
Dust	*S. diana*	0	5/0	0	0	0	0	5

[1] Regurgitated plant material, primarily grass, presumably from Canids

TABLE 2. Total number of *Speyeria diana* and *S. cybele*, summer across years, detected on restored sites and control sites (n = 3 plots/treatment) on the Ouachita National Forest during 2000-2002.

Species	B-1[a]	B-2	B-3	Control
S. diana	19	39	13	2
S. cybele	41	126	30	4

[a] B-1, B-2, and B-3 correspond to 1st, 2nd, and 3rd growing seasons post-burn.

TABLE 3. Response of nectar resources to shortleaf pine-bluestem restoration on the Ouachita National Forest during 2000–2002. Mean numbers of nectar resources per 300 m² plots in restored and control stands (n = 3 plots/treatment). Letters represent significantly different means in a 1-way ANOVA with REGWQ at $P < 0.1$ (SAS Inst. Inc. 1988:598). Because abundance values varied greatly within treatments, data were rank transformed prior to analysis.

		B-1		B-2		B-3		Control		
Year	Month	x	SE	x	SE	x	SE	x	SE	P
2000	April	84.7A	45.5	960.0B	532.1	154.7A	62.3	150.7A	12.4	0.0278
	June	1018.3A	364.0	420.3A	134.9	399.3A	172.3	49.7B	15.4	0.0191
	August	417.7A	157.3	583.0A	312.6	56.3B	41.4	3.7B	0.7	0.0011
	October	746.3A	66.4	84.3B	45.9	59.3B	21.9	7.3C	5.0	0.0010
2001	April	0.0A	0.0	1234.3B	415.3	661.3B	391.2	117.7C	42.7	0.0003
	June	1492.7A	859.8	462.7A	320.9	215.3A	82.7	26.7B	8.1	0.0088
	August	1735.7A	669.6	588.7B	127.5	483.0B	218.5	24.3C	8.8	0.0011
	October	2745.0A	604.9	3219.0A	1605.5	515.3B	106.2	183.7B	130.4	0.0047
2002	April	241.0A[1]	77.1	17.0A	15.0	270.3A	41.7	197.0A	187.1	0.2593
	June	1067.7A	601.2	1316.7A	417.1	721.3A	99.3	49.7B	20.3	0.0595
	August	768.3A	102.2	702.7A	137.9	156.0B	57.3	9.0B	2.1	0.0011
	October	4587.3A	2987.2	1746.7A	689.1	719.3AB	355.0	35.0B	8.3	0.0181

[1] Plots scheduled to be burned prior to April 2002 surveys were not burned until after the April surveys were complete and thus represent the fourth growing season post-fire.

Within the restored treatments the 1st year post-burn sites generally supported the most nectar resources and the 3rd year post-burn treatments the least, in all months and years (Table 3). Many significant differences support this overall pattern (Table 3). The only exceptions were those noted above and three of 12 instances when the abundance of nectar resources on the 2nd year post-burn sites exceeded those on the corresponding 1st year post-burn sites.

Viola spp., the only larval host of *Speyeria* spp. (Opler and Krizek 1984), were abundant in the restored treatments and uncommon in the controls. *Viola pedata* L. (bird's foot violet) was the predominant species, although *Viola sagittata* Ait. (arrow-leaved violet) was also present in more mesic sites. These and additional species were also present in adjacent habitats. Based on the nectar resource surveys, *Viola* flowers were more abundant on treatment transects (Table 4) than on control transects, and significant differences existed across treatments ($\chi^2 = 71.0$, df = 3, $P < 0.001$).

TABLE 4. Mean number of *Viola* spp. flowers (flowers/300 m²) detected during June surveys on restored sites and control sites (n = 3 plots/treatment) on the Ouachita National Forest during 2000–2002.

Year	B-1	B-2	B-3	Control
2000	79.7	52.2	2.92	6.2

DISCUSSION

Restoration treatments effectively altered forest structure to more closely resemble the inferred pre-European structure (Sparks *et al.* 1999, Thill *et al.* 2004). The primary changes were reduced canopy cover, elimination of most midstory vegetation, and the restoration of a dense herbaceous ground cover (Thill *et al.* 2004). In addition, the reintroduction of frequent prescribed fire reduced the litter layer, removed dead herbaceous vegetation, and stimulated flowering of a diverse array of herbaceous angiosperms (Sparks *et al.* 1998).

In fire-maintained pine forests in eastern Texas (Rudolph and Ely 2000), the complete data set for Arkansas (Thill *et al.* 2004), and migrating monarchs in Arkansas (Rudolph *et al.* 2006) butterfly abundance was significantly greater in sites with a frequent fire regime compared to fire-suppressed sites. Furthermore, butterfly abundance was greatest in the first growing season following late winter-early spring prescribed fires and declined markedly in successive growing seasons, at least through the first few years (Rudolph *et al*, unpub. data). These changes in butterfly abundance were correlated with similar abundance patterns for the nectar resources (Thill *et al.* 2004, Rudolph *et al.*, unpub. data). A similar pattern was detected in fire-maintained pine forests in Texas (Rudolph and Ely 2000). In a ponderosa pine ecosystem in Arizona, also a

fire-maintained system, Waltz and Covington (1999) found parallel responses of butterflies and nectar plants following thinning and prescribed fire.

Both species of *Speyeria* and their primary nectar resources were essentially absent from control treatments, but more abundant on the restored treatments for at least three years post-fire. We suggest that the increased abundance of both *Speyeria* was due to the significantly increased availability of nectar resources in the restored treatments. The increased abundance of *Speyeria*, especially *S. diana*, is consistent with observations of *S. diana* throughout the Interior Highlands. *Speyeria diana* was characterized by Carleton and Nobles (1996) as rare and local, and by Moran and Baldridge (2002) as widespread and local in the Interior Highlands. They associated occupied sites with disturbance, including fire, and Moran and Baldridge further noted their association with high quality nectar resources. We observed similar patterns during 5 years of field work in the Ouachita Mountains. In addition, our observations, and those reported by Carlton and Nobles (1996) and Moran and Baldridge (2002), beyond the restoration landscape are primarily of one or a few individuals. In marked contrast, we have observed, on several occasions, up to 12-16 males on a single black bear (*Ursus americanus* Pallas) or coyote (*Canis latrans* Say) fecal deposit, and 4-6 females on a single thistle (*Cirsium discolor*) plant with multiple inflorescences, within the restored shortleaf pine/bluestem landscape. The more general occurrence of nectar resources across the landscape, including those most frequently utilized by *Speyeria*, following restoration and prescribed fire is consistent with these observations. Without restoration, abundant nectar resources of the frequently used species are generally restricted to disturbed sites including road verges, recently disturbed logging sites, and utility rights-of-way (Rudolph *et al.* pers obs.).

Unlike the pattern for all butterflies, the abundance of both species of *Speyeria* was greatest in the second growing season post-fire. Several hypotheses, not necessarily mutually exclusive, are available that may explain this pattern. First, *Speyeria* may require more than one growing season to fully re-colonize a site. If substantial mortality of immature stages occurs during fire events, re-colonization by volant adults may not be complete within the first flight period following fires. Second, and related to the first, adult *Speyeria* abundance may be a consequence of enhanced on-site reproduction due to the abundance and/or vigor of the larval host, *Viola* spp., following fires. Third, the preferred nectar resources used by both *Speyeria* peak following the first growing season post-fire, and *Speyeria* abundance is simply tracking nectar resources. Fourth, the majority of the increase in *Speyeria* abundance in the second growing season post-fire compared to the first was found in 2002. It is possible that the abundance of *Speyeria* in the first year post-fire plots in 2002 was depressed due to a landscape effect resulting from the somewhat peripheral location of the first year post-fire sites in the overall restoration area in 2002.

Speyeria used a limited subset of the nectar resources potentially available or used by the overall butterfly fauna. More than 88% of nectaring observations for *S. cybele* were from 11 species, and more than 95% of observations for *S. diana* were from only 8 nectar plant species. These numbers represent a small minority of the 154 species of nectar plants used as nectar sources by the entire butterfly fauna during the flight period of *S. cybele* and *S. diana* (Rudolph *et al.* unpub. data). Moran and Baldridge (2002) reported similar results. These data suggest that *Speyeria* populations in the Interior Highlands, and especially *S. diana*, may be dependent on the availability of a limited number of plant species that provide high quality nectar resources. In the absence of frequent fire, suitable nectar resources are rare and fragmented, and may be able to support only localized and small populations of *S. diana*. Moran and Baldridge (2002) recorded the greatest abundances of *S. diana* in remnant prairie habitat with abundant floral resources, and wetlands with abundant *Cephalanthus occidentalis* L., a preferred nectar resource for *Speyeria* in areas peripheral to the core of the Ouachita Mountains. These habitats are infrequent in our study area. *Speyeria cybele*, perhaps due to its smaller size, may be less specialized with regard to high quality nectar resources and consequently is considerably more abundant in fire-maintained pine habitats (this study) as well as in fire-suppressed habitats throughout the Ouachita Mountains (Rudolph *et al.* pers. obs.).

It is important to realize that this discussion is based entirely on observations of adult *Speyeria*. Despite considerable effort, we have been unable to identify the larval hosts or habitats of either species in the Ouachita Mountains. *Viola* spp., the only known host of larval *Speyeria* spp., are abundant in diverse habitats in the Ouachita Mountains. *Viola pedata* is abundant in the fire-maintained pine community, less so in fire-suppressed sites, and several other species are common to abundant in more mesic sites on north-facing slopes and along drainages (pers. obs.) Whether *Speyeria* spp. use *Viola* spp. in fire-maintained communities or adjacent habitats remains an important question. Several females were observed exhibiting possible

ovipositing behavior (Harris 1972) in fire-maintained pine habitat in the vicinity of *V. pedata*, but actual egg laying could not be verified.

Based on these data and observations, we agree with Moran and Baldridge (2002), that loss of high quality nectar resources may be the primary cause of population declines and range contractions in *S. diana*, and further suggests that similar considerations may apply to *S. cybele*, at least in the Ouachita Mountains. Lepidoptera exhibit two strategies in relation to the nutritional reserves used to mature eggs (Tammaru and Haukioja 1996). At one extreme (capital breeders) reserves accumulated during the larval stage are used; at the other extreme (income breeders) reserves acquired by adult foraging are used. Increased fecundity and longevity are dependent on adult food intake in income breeders (Gilbert 1972, Fischer and Fielder 2001). *Speyeria*, at least the longer lived species, are best characterized as income breeders with increased fecundity dependent on adult feeding (Boggs and Ross 1993, Boggs 1997).

We suggest that reduced fecundity due to reduced nectar abundance and quality is the proximate cause of the observed low populations of *Speyeria*, especially *S. diana*, throughout most of the Interior Highlands. We further suggest that the Interior Highlands, much of which remains forested, have experienced a massive decline in nectar resources since the arrival of Europeans, due primarily to changes in vegetation structure resulting from alteration of the pre-European fire regime. The resulting suppression of the herbaceous flora within the original fire-maintained pine communities has had negative effects on the overall butterfly fauna (Thill *et al.* 2004). A prescribed fire regime that restores a fire-maintained pine/bluestem community on a landscape scale in the Ouachita Mountains has been demonstrated to result in at least a local increase in *Speyeria* spp., including *S. diana*, a species of conservation concern. Additional research addressing competition between the two *Speyeria* species, larval biology especially in relation to host plants, mimicry relationships with the Pipevine Swallowtail, *Battus philenor* (L.), and effects of landscape parameters would provide additional insight into the abundance and ecology of *Speyeria* in the Interior Highlands.

Fire, including prescribed fire, has profound effects on the composition and structure of plant communities, and consequently on butterfly faunas. The effects on butterfly faunas are a complex interplay of effects on host plants (Kwilosz and Knutson 1999), nectar resources (Shuey 1997, Rudolph and Ely 2000), mortality of immature stages (Dana 1991, Swengel 1995, 2001), microclimate (Rudolph and Ely 2000), and other interactions. Often, these effects are beneficial, at least in maintaining populations of species that have declined due to habitat alteration in the absence of fire (Williams 1995, Shuey 1997). In the increasingly fragmented landscapes that characterize much of the planet, fire can affect entire habitat patches with negative results. This is often the case in small prairie remnants in North America (Dennis and Eales 1997). However, the landscape scale restoration of a frequent fire regime on the Ouachita National Forest appears to increase populations of most butterfly species (Thill *et al.* 2004, Rudolph *et al.* 2006) including *S. diana* and *S. cybele*.

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CLUTCH SIZE VARIATION IN *URANIA BOISDUVALII* (GUERIN) (URANIIDAE: URANIINAE).

Additional key words: Moth, gregarious oviposition, Lepidoptera

The moth subfamily Uraniinae is represented by only one genus in the New World, *Urania* Fabricius. This genus contains six species, all with diurnal habits and iridescent colors. Two endemic species of this genus inhabit Cuba: *Urania boisduvalii* (Guérin), distributed throughout the island, and *Urania poeyi* (Gundlach), restricted to eastern Cuba.

In general, the clutches of the Lepidoptera present three patterns based on the number of eggs laid by the female during oviposition: i) eggs laid singly; ii) small clutches of up to 20 eggs; iii) large clutches with more than 20 eggs (García-Barros 2000).

Urania females oviposit at dusk, *ca*. 1700 h (Smith 1992). Guppy (1907) found that *Urania leilus* (L.) laid eggs singly or in pairs on the underside of a leaf. Smith (1992) observed that in *Urania fulgens* Walker the eggs are laid singly or in clutches of up to 90 eggs and *Urania boisduvalii* laid single eggs on the midrib on the underside of large leaves of *Omphalea* spp.

In August 2001, Dr Emanuel Mora brought one of the authors (A. Barro) three leaves of *Omphalea trichotoma* Mueller-Argoviensis that he found with clutches of thousands of eggs of *Urania boisduvalii* in Playa El Holandés, Península de Guanahacabibes, Pinar del Río Province in western Cuba (21°50.07' N, 84°46.00' W). For this reason, we decided to study clutch size in *Urania boisduvalii*. We selected two sites for our field studies: the already mentioned Playa El Holandés, and Piedra Alta, Santa Cruz del Norte, La Habana Province (23°10.04' N, 81°59.15' W). This work was conducted during June and August 2003 and February and May 2004 in Playa El Holandés, and between October 2002 and December 2004 in Piedra Alta at biweekly intervals.

During the study, we chose 50 plants of *Omphalea trichotoma* in each locality and checked each leaf on its underside. We recorded the number of eggs on each leaf, the way in which they were laid (singly or in clutches) and made notes about the hour of oviposition and behavior of the larvae.

We found 302 leaves with eggs (Figure 1). From this total, 247 leaves (82%) had only one egg, 13 leaves had a pair of eggs on the underside (4%) and 32 leaves (14%) had clutches of 3 to 179 eggs. In addition, we observed two leaves with 432 and 500 eggs and eight leaves with more than 2000 eggs each one. On the leaves with more than 2000 eggs, the eggs were laid in many layers and it was impossible to count their exact number. In both localities we found the same results.

The clutches bigger than 100 eggs could be the result of gregarious oviposition, a phenomenon described in other lepidopterans (Mallet & Jackson 1980, Goodfray *et al*. 1991, Sourakov 1997, Reed 2003, Fordyce & Nice 2004). Although we did not observe different females of *Urania boisduvalii* contributing to a collective egg clutch, we have two reasons that support this idea. Smith (1992) reported a large number of eggs in the ovarioles of migratory *Urania fulgens* (*ca*. 300–400) and only 15–30 eggs in the ovarioles of sedentary females of this species. We consider that *Urania boisduvalii* have similar characteristics to *Urania fulgens* in the number of eggs per ovariole because we counted the number of eggs per ovariole in four females and found that *U. boisduvalii* females have between 15 and 35 eggs per ovariole (22.5± 5.4). Furthermore, during our study at Playa El Holandés on several occasions around 60 females were observed visiting a host plant site and flying around the host plant and ovipositing on *Omphalea* leaves. However, at present we cannot prove that females of *Urania boisduvalii* produce collective egg clutches. In any case, our observations are the first report of great variation in clutch size for the family Uraniidae.

Stamp (1980) summarizes some hypotheses about the

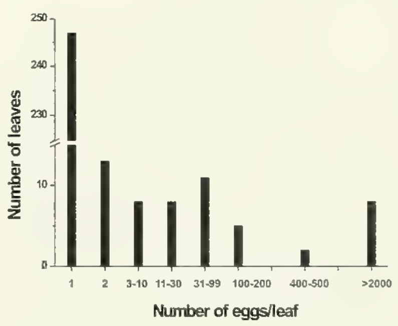

FIGURE 1. Variation in the number of eggs of *Urnia boisduvalii* per leaf of *Omphalea trichotoma*

adaptive value of gregarious oviposition in butterflies. Some of these hypotheses might explain the large egg clutches laid by *Urania boisduvalii*. Prevention of egg desiccation and protection against predators and parasitoids seem to be two possible hypotheses. In

addition, we found at both study sites that the first and second instars of *Urania boisduvalii* display a gregarious behavior. Perhaps this behavior was facilitated by gregarious oviposition, as suggested by Sillén-Tullberg (1988) for many species of butterflies.

We cannot explain why *Urania boisduvalii* displays such a large range in egg clutch size. Although we have not been able to demonstrate that this species presents gregarious oviposition, finding clutches with more than 2000 eggs in an uraniid moth, supports the idea that in the Lepidoptera this phenomenon is common, as suggested by Reed (2005).

We thank Emanuel Mora for providing us the first leaf of *Omphalea trichotoma* with egg clutches of *Urania boisduvalii*. We also thank to Dr Frank Coro for his comments about the manuscript. We also thank Dr David Arhenholz and one anonymous reviewer for comments.

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EGG VIABILITY AND LARVAL CONTRIBUTION TO FECUNDITY OF *PARNASSIUS SMINTHEUS* DOUBLEDAY (PAPILIONIDAE)

Additional key words: life history, reproduction, Rocky Mountain Apollo

Fecundity and egg viability are important components of life history affecting population dynamics and persistence as well as being a central factor in evolution. Despite its basic nature, estimates of fecundity for Lepidoptera are not common (Hunter 1995). Here we briefly present estimates of egg viability and fecundity primarily due to larval resources for the Rocky Mountain Apollo butterfly *Parnassius smintheus* Doubleday, 1847.

We collected 146 female butterflies from two large meadows (sub populations P & Q, see Matter *et al.* 2000) along Jumping Pound Ridge, Kannanskis, Alberta, Canada (51°57'N, 114°54'W, ~2100 m). All *P. smintheus* encountered were removed on six occasions (July 20, 23, 30, 31 and August 11, 19) during the adult flight season of 2005 (~18 July–24 August). We collected ten additional females from nearby Powderface Ridge (Matter and Roland 2002) on August 6th 2005. The removals on Jumping Pound Ridge are part of a larger experiment examining spatial population dynamics. Upon capture, we placed individual butterflies in a glassine envelope and took them to The University of Calgary's Barrier Lake Field Station (~1400 m) where they were kept in the envelopes at ambient conditions. After the female's death, we counted the number of eggs laid by each butterfly. Because butterflies were removed from meadows frequently, each was captured fairly shortly (1–10 d) after its emergence. *Parnassius smintheus* continues to develop eggs in the adult stage (C. Guppy, personal communication). Thus, the number of eggs produced here should largely represent fecundity based on larval resources, rather than total fecundity including additional eggs produced from nectar resources during the adult stage. Additionally, the mating status of females was assessed by the presence or absence of a sphragis which males affix to females during copulation to prevent additional mating by other males (Bird *et al.*

1995).

We examined egg viability for a subset of females and compared viability among mated and unmated females. Eggs from all females were kept at ambient temperature until September 4. After that they were refrigerated in a humid relaxing chamber at ~5 °C until use in mid December. Between 3 and 28 eggs (X = 12.2) from 32 females (25 mated and 7 virgin) were placed on wetted filter paper in individual Petri dishes and kept at room temperature (~25 °C). Although some larvae began to eclose immediately upon the addition of water, most hatched after 4–5 days. To ensure that hatching was complete, we kept the filter paper moist and waited 3 weeks to examine number of larvae that eclosed.

We compared egg production among the three populations and between mated and unmated females using one-way analysis of variance. To assess any effect of the time between captures on the number of eggs produced we used linear regression.

Populations differed in the number of eggs produced by females ($F_{2,153}$ = 5.52, P = 0.01). Likely due to differences in phenology and our frequent removals, the mean numbers of eggs produced by females from the two Jumping Pound Ridge sub-populations (19.3 ± 2.1 (Std. Error, here and throughout) and 10.8 ± 2.3) were much greater than butterflies from Powderface Ridge (1.1 ± 0.7). All further analyses exclude the Powderface Ridge butterflies. There was no difference in the mean number of eggs laid by mated (18.0 ± 2.1) or unmated females (15.2 ± 2.8; $F_{1,144}$ = 0.52, P = 0.47), indicating that male-donated nutrients likely play little or no role in female fecundity for this species (Boggs 1990, 1997). The number of eggs laid by butterflies collected on different dates showed significant variation ($F_{5,140}$ = 4.93, P < 0.01). The greatest numbers of eggs were produced by females collected on July 30 and 31. Surprisingly, the number of eggs laid increased with the number of days between butterfly removals ($F_{1,141}$ = 16.16, P < 0.01). Thus, the observed number of eggs produced by females did not decrease due to prior oviposition by older females collected after longer intervals. In contrast, this result suggests that longer access to adult nectar resources may increase egg production (see below).

Across all butterflies from the two Jumping Pound Ridge populations, the mean number of eggs produced was 17.1 ± 1.7 (Figure 1). The distribution was highly skewed, ranging from 35 butterflies that produced no eggs to one female that produced 95 eggs. If the data are limited to mated females the mean number of eggs produced increases slightly to 18.0 ± 2.1. The number of eggs produced by *P. smintheus* was much lower than estimates for *Euphydryas editha* and *Melitaea cinxia* (Boggs and Nieminen 2004). Watanabe and Nozato (1986) reported a similar mean of 17.8 ± 4.9 mature eggs from dissections of 17 newly emerged spring generation *Papillio xuthus*. Newly emerged butterflies from later generations and from *P. machaon* showed over twice as many mature eggs. The low reproductive output seen for *P. smintheus* relative to other Papillionids is likely a function of the lack of adult nutrition (nectar) provided in our study combined with continued egg maturation by adults. Lack of adult nectar resources may limit both lifespan and egg maturation (Boggs 1997). Thus, the reproductive output seen here largely represents the contribution due to larval resources, and is not an estimate of total potential fecundity. This result further emphasizes the importance of adult nectar resources for population processes (Matter and Roland 2002).

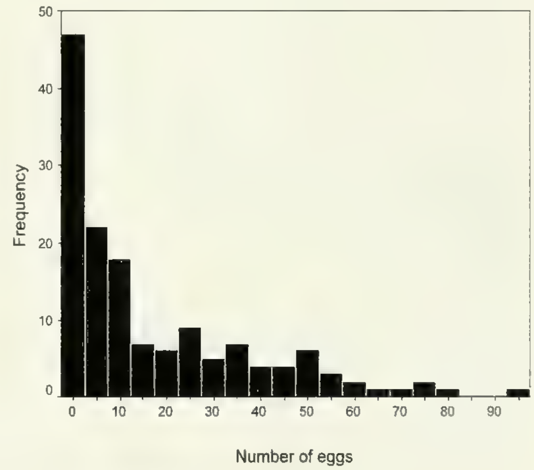

FIGURE 1. Frequency distribution of the number of eggs laid by female *Parnassius smintheus* from two populations along Jumping Pound Ridge.

A mean of 46.3 ± 8.2 % of the eggs from mated females produced larvae (range 0–100%). No larvae were reared from eggs from females without a sphragis. This result confirms that the sphragis generally is not lost, and the presence of a sphragis can be used to confirm mating status. Dissection of 5 eggs from one mated female revealed 3 live pharate first instar larvae and 2 incompletely developed larvae. As these butterflies overwinter as pharate first instars (Guppy and Shepard 2001) the fate of the incompletely developed eggs is unclear. These eggs, presumably produced later in the season, either die or overwinter. The incomplete development may have been due to

some eggs being subjected prematurely to a cold environment. It is unclear to what degree this incomplete development occurs under natural conditions.

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SOURWOOD DEFOLIATION BY LETTERED SPHINX (*DEIDAMIA INSCRIPTA*) IN GREAT SMOKY MOUNTAINS NATIONAL PARK (LEPIDOPTERA: SPHINGIDAE)

Additional key words: Black bear, grape.

The Lettered Sphinx, *Deidamia inscripta* (Harris), is a familiar, widespread moth that occurs from South Dakota, extreme southern Quebec, and Massachusetts to northern Florida and Mississippi (Hodges 1971, Covell 1984). It is a univoltine, early season sphingid, flying from late April through mid May over much of its range (Hodges 1971). Reported hosts include grape (*Vitis*), ampelopsis (*Ampelopsis*), and Virginia creeper (*Parthenocissus*), all members of the Vitaceae (Forbes 1948, Hodges 1971, Covell 1984). Here we report widespread use and defoliation of a heath, sourwood (*Oxydendrum arboreum* (L.) DC) (Family Ericaceae), in the Appalachians.

DLW first noticed the presence of *Deidamia* on sourwood in West Virginia in 1995 near Parsons, Tucker County, West Virginia. More than a dozen larvae were collected on a small 2 m high tree, but the caterpillars soon consumed all the foliage that had been gathered for them, and as a result the identification of both foodplant and sphingid remained unknown. In 2000 when DLW started visiting Great Smoky Mountains National Park as part of the Park's "All Taxa Biodiversity Inventory," the sphinx was again encountered in large numbers—this time both the host and moth were identified to species. May visits to the Park in 2001–2003 yielded enormous numbers of the caterpillar from sourwood, especially from drier, open woodlands where Virginia pine (*Pinus virginiana* P. Mill.) was a dominant tree. During the third week of May in 2003, Eric Hossler and DLW observed numbers commonly in excess of 20–30 late instar *Deidamia inscripta* per shrub along the Foothills Parkway East, above Cosby, Cocke County, Tennessee—many smaller plants were defoliated by the larvae. KL first noted *Deidamia* in the Park more than a decade earlier. The following are two excerpts from the Park's "Observations Database."

1988-May-28 Location: Chilhowee Mt. along Foothills Parkway and west end of the Park. Observation: About half of the smaller trees of this species [*Oxydendrum*] are significantly or entirely defoliated. Examined several, found only 1 large sphinx-type larva, green. This defoliation was not observed in 1986 or 1987. K. Langdon.

1990-May-20 Location: Foothills Parkway Walland to Look Rock Observation: Most Sourwoods at least partially defoliated. On some, defoliation is 100%, only leaf mid-veins left. Collected green sphinx larvae for rearing, but they died. K. Langdon.

We report here an instance of large-scale defoliation in the spring of 2004, again along the Foothills Parkway East. The pictures shown here (figs. 1–3) were taken below the summit of the Parkway (N35°49.227' and W83°13.032'). Most of the smaller, 2–4m shrubs growing along the road had been stripped or were soon to be defoliated by the caterpillars. Road surfaces near

FIGURES. 1-6. All images taken along the Foothills Parkway East, near Cosby, Cocke County, Great Smokies Mountain National Park, 16 May, 2004. **1**. Sourwood shrubs stripped of foliage. **2**. This 2 m plant had 49 actively feeding larvae. **3**. Branch at base of shrub in foreground of Fig. 1: 12 of the 18 larvae counted on the branch are visible (arrows). **4**. Regurgitating caterpillar. **5**. Vomit released by held caterpillar. **6**. Alarm posture of *Deidamia inscripta* last instar.

defoliated trees had densities of up to 8 smashed larvae per square meter. One 20 m stretch of the Parkway had 118 smashed or wandering caterpillars. Immediately upslope from this section of the Parkway, a sourwood tree (approximately 4.5 m in height) yielded 91 caterpillars. Given the number of caterpillars smashed along the highway and wandering in the vicinity of the aforementioned shrub, it is likely that many caterpillars had already matured or departed in search of additional foliage. On this same tree, 18 larvae were counted on a limb near the ground (fig. 2). The shrub shown in fig. 3 yielded 49 larvae—it, too, was destined to be stripped. We estimate that the majority of the larvae along the Parkway were in their last two instars on 15–17 May, although few had obtained their final mass. Because many younger caterpillars were present and one adult Lettered Sphinx was seen at light nearby (15 May at Cosby Creek), it was evident that the sourwood in the Park would continue to be impacted for 2–4 weeks beyond what we show here. Along the 6-mile length of the Foothills Parkway East, shrubs and plants under 3 m were mostly or completely defoliated by 17 May, 2004. Many larger trees, i.e., those in excess of 6 m, appeared as if they would come through the season with some intact foliage. Grape, also growing at the site, had Lettered Sphinx caterpillars, but in far lower densities—a search of one patch yielded eight *Deidamia* in five minutes. In contrast to the sourwood plants along the Parkway, grape vines had little to no obvious feeding damage.

Brian Scholtens (personal communication), who ran a blacklight bucket trap along the Parkway on the night of 15 May, noted five *Deidamia* caterpillars about his bucket trap the following morning. Prior to this, he had never noted multiple sphingid caterpillars anywhere in North America while servicing light traps. Upon returning home from blacklighting in the west end of the Park at 0030 h, Brian Scholtens and DLW noted over 50 *Deidamia* caterpillars crawling along a 6-mile stretch of the Little River Road east of Cades Cove, Sevier County, TN. All were counted in our headlight beams, while traveling at speeds mostly in excess of 40 mph. Neither one of us had ever experienced a phenomenon such as this.

Given the remarkably high densities reported here, it is odd that sourwood would have gone heretofore unnoticed as a host for such a large and familiar insect. What we find equally extraordinary and perplexing is that densities appear to be chronically high—one wonders why natural enemies, be these birds or parasitoids, are not extracting higher tolls on these caterpillars. KL recalls an account by Arthur Stupka, the GSMNP naturalist from 1938 to 1963, mentioning "black bears feeding on caterpillars in sourwood" (although we have been unable to locate an original source with Stupka's observations).

Deidamia caterpillars are quick to throw their body an alarm display: the larva releases its grip, arches the head back over the abdomen, and holds the thoracic legs up and splayed apart (Fig. 6). Green fluid may be pushed from the mouth (Fig. 4). If agitated further, the caterpillar produces considerable amounts of a watery, but somewhat sticky, green vomit (Fig. 5). DLW found it bitter to the taste (n=3), but not as bitter as the foliage of sourwood itself. It was somewhat difficult to wash away, being either mucilaginous or basic. Additionally, the caterpillars attempted to bite when held or are otherwise harassed.

Also noteworthy is the taxonomic jump in foodplant choice from Vitaceae to Ericaceae. While it would seem unlikely that the populations on sourwood are evolutionarily distinct, it certainly wouldn't hurt to have a closer look at sourwood-feeding populations. Larval vouchers, collected from both grape and sourwood, have been deposited at the University of Connecticut.

Rene Twarkins assembled the plate for this paper. Jeanie Hilten and Discover Life in America provide lodging and facilitated DLW's trips to the Park.

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NECTAR SOURCE RECORDS FOR *LIBYTHEANA CARINENTA* (NYMPHALIDAE: LIBYTHEINAE)

Additional key words: butterfly gardening, flower color, flower visitation, nectaring, snout butterfly

The American Snout Butterfly, *Libytheana carinenta* (Cramer), is known to feed on water from moist sand and soil (Howe 1975, Iftner et al. 1992, Kawahara 2003, Dirig unpubl.), and at dung, fruits, human perspiration, secretions from aphids, and various flowers (Kawahara 2001, 2006b). Flower nectar is rich in water, monosaccharides, and amino acids (Watt et al. 1974), and butterflies use nectar as an immediate energy source, or store it as fat (Opler & Krizek 1984). Female butterflies assimilate these nutrients for egg maturation (Stern & Smith 1960), and sugars can increase the longevity of adult Lepidoptera (Norris 1934).

Shields (1972, 1985) summarized flower visitation records for *L. carinenta*, but many additional nectaring observations were discovered during a recent review of the biology and natural history of the Libytheinae (Kawahara 2006a, b). Shields (1985) reported 19 flowering plants in 14 families that were used as nectar sources for *L. carinenta*; while we report 66 plants in 27 families (Table 1). Many of our records are from publications that appeared after Shields' work, but there are also numerous reports that were not included in his studies. We supplement published records with Harry Pavulaan's personal observations in Maryland and Virginia; and with Robert Dirig's personal observations at Cape May (Cape May County), New Jersey, and in the Finger Lakes Region (Tompkins and Schuyler Counties) in New York.

We also expanded upon Shields' studies by determining flower color for each record. Saunders (1932) and Opler & Krizek (1984) reported flower color preference for many butterflies, but their reports did not include *L. carinenta*. The purpose of this publication is threefold: (1) to provide a list of flower visitation records for *L. carinenta*; (2) to update all plant records to follow a modern classification of flowering plants; and (3) to determine the color of flowers visited. We did not examine floral color variation within this butterfly's geographic distribution because many published sources did not specify where observations were made.

Butterfly taxonomy follows a recent revision of the Libytheinae (Kawahara, accepted), plant names accord to Kartesz & Kartesz (1980), and plant family classification follows APG II (2003). Flower color was determined using Gray's Manual of Botany (Fernald 1987), in addition to regional floral guides (Kearney & Peebles 1960, Long 1971, Scoggan 1978, Taylor 1998, Jones 2005). Many flowers listed in our studies have one or more color variants, and we were unable to determine the specific color for some of the flowers visited. We are therefore including all possible color variants for each plant unless we had specific information on the color of the flower from which the butterfly was recorded.

We recorded 17 flowering plant species of the Asteraceae (25.8%), 7 of the Rosaceae (10.6%), 4 of the Apiaceae (6.1%), 4 of the Fabaceae (6.1%) and 4 of the Lamiaceae (6.1%); the remaining plant families were each represented by less than 3 species (< 4.6%). These results are consistent with floral visitation records obtained for butterflies in central Illinois, which indicated that the five most butterfly-visited plant families are Apiaceae, Asteraceae, Fabaceae, Lamiaceae, and Rosaceae (Robertson 1928, Tooker et al. 2002).

FIGURE 1. *Libytheana carinenta* nectaring at Buttonhead Goldenrod (*Euthamia tenuifolia*, Asteraceae) at Higbee Beach, Cape May Co., N.J., 7 Oct. 2004, photo by R. Dirig.

Our results are also consistent with flower visitation records of nymphalines and pierids, which are known to favor white or yellow flowers (Opler & Krizek 1984). Twenty-eight of our flower visitation records were on white flowers (42.4% of flowers recorded were truly white), 10 (15.2%) were yellow, 4 (6.1%) were purple, 1 (1.5%) was pink, and 1 (1.5%) was red. Due to color variants, flower visitation records may constitute up to 46 (69.7%) plant species that are white or partially

TABLE 1. Flower visitation records for *Libytheana carinenta*, and the typical flower color for each plant. Taxa are listed alphabetically.

Plant family	Plant genus & species	Flower color	Reference
Acanthaceae	*Avicennia germinans* (L.) L.	White or yellow	Heitzman & Heitzman (1972)
Amaranthaceae	*Gomphrena globosa* L.	White or red	Dirig (pers. obs., NJ)
Anacardiaceae	*Rhus copallina* L.	Yellow	May (1987), Dirig (pers. obs. NJ)
Apiaceae	*Cicuta maculata* L.	White	Robertson (1928)
	Daucus carota L.	White	Iftner et al. (1992)
	Pastinaca sativa L.	Yellow	Robertson (1928)
	Sium suave Walt.	White	Robertson (1928)
Apocynaceae	*Apocynum cannabinum* L.	White	Opler & Krizek (1984)
	Asclepias incarnata L.	Pink or red	Robertson (1928)
	Asclepias syriaca L.	Pink or purple	Iftner et al. (1992)
Asteraceae	*Aster pilosus* Willd.	White and yellow	Robertson (1928), Dirig (pers. obs., NY)
	Aster vimineus Lam.	White or pink	Iftner et al. (1992)
	Baccharis glutinosa (Ruiz & Pavon) Pers.	White	Opler (1998)
	Baccharis halimifolia L.	White	Dirig (pers. obs., NJ)
	Baccharis sarothroides Gray	White	Shields (1985)
	Bidens alba var. radiata Schultz-Bip.[a]	White and yellow	Floridata (2006)
	Bidens aristosa (Michx.) Britt.	Yellow	Iftner et al. (1992)
	Centaurea maculosa Lam.	Purple	Dirig (pers. obs., NY)
	Chrysanthemum sp.	Yellow and pink	Dirig (pers. obs., NJ)
	Chrysothamnus nauseosus (Pallas) Britt.	Yellow	Pyle (1981)
	Cirsium arvense (L.) Scop.	Purple	Sedman & Hess (1985)
	Eupatorium fistulosum Barratt	Pink or purple	Floridata (2006)
	Eupatorium perfoliatum L.	White	Iftner et al. (1992)
	Euthamia tenuifolia (Pursh) Greene	Yellow	Dirig (pers. obs., NJ)
	Senecio douglasii DC.	Yellow	Shields (1985)
	Solidago canadensis L.	Yellow	Pavulaan (pers. obs., MD, VA)
	Solidago sp.[b]	Yellow	Opler & Krizek (1984), Dirig (pers. obs., NJ)
	Verbesina encelioides (Cav.) Benth & Hook f. ex Gray	Yellow	Neck (1984)
Basellaceae	*Anredera cordifolia (Ten.) Steenis*	White	Gable & Baker (1922)
	Anredera leptostachys (Moq.) Steenis	White	Shields (1985)
Boraginaceae	*Cordia sp.*	White, pink or red	Hernández (2004)
	Tournefortia hirsutissima L.	White	Hernández (2004)
Brassicaceae	*Berteroa incana (L.) DC.*	White	Iftner et al. (1992)
Clethraceae	*Clethra alnifolia L.*	White or pink	Opler & Krizek (1984)
Cornaceae	*Cornus sp.*	White, pink or purple	Pyle (1981)
Euphorbiaceae	*Croton sp.*	White	Shields (1972)
Fabaceae	*Eysenhardtia polystachya* (Ortega) Sarg.[c]	White	Gable & Baker (1922)
	Eysenhardtia texana Scheele	White or yellow	Neck (1983)
	Melilotus alba Medic.	White	Shields (1985)
	Prosopis glandulosa Torr.	White or yellow	Wauer (2002)

TABLE 1. (continued)

Plant family	Plant genus & species	Flower color	Reference
Lamiaceae	*Mentha arvensis* L.	White or pink	Dirig (2005)
	Origanum vulgare L.	White	Pavulaan (pers. obs., MD, VA)
	Pycnanthemum flexuosum (Walt.) B. S. P.	White or purple	Robertson (1928)
	Salvia guaranitica A. St.-Hil.	Purple	Dirig (pers. obs., NJ)
Lobeliaceae	*Lobelia cardinalis* L.	Red	Ross (1990)
Loganiaceae	*Buddleja davidii* Franch.	White	Dirig (pers. obs., NJ)
Malvaceae	*Tilia sp.*	White	Shields (1985)
Oleaceae	*Ligustrum vulgare* L.	White	Shields (1985)
Poaceae	*Heteropogon contortus (L.)* Beauv. ex Roemer & Schultes	White or yellow	Bailowitz & Brock (1991)
	Sorghum sp.	White or yellow	Parman (1926)
Polygonaceae	*Eriogonum sp.*	White, yellow or pink	Shields (1972)
Ranunculaceae	*Clematis drummondii* Torr. & Gray	White	Neck (1984)
	Clematis vitalba L.	White	Shields (1985)
Rhamnaceae	*Condalia sp.*	Yellow	Gilbert (1985)
Rosaceae	*Potentilla fruticosa* L.	Yellow	Iftner et al. (1992)
	Prunus americana Marsh.	White	Ajilvsgi (1990)
	Prunus caroliniana (P. Mill.) Ait.	White	Shields (1985)
	Prunus persica (L.) Batsch	Pink	Pyle (1981)
	Rubus fruticosus L.[d]	White	Bubna (1897)
	Rubus idaeus L.	White	Scudder (1889)
	Spiraea latifolia (Ait.) Borkh.	White or pink	Landry (1987)
Rubiaceae	*Cephalanthus occidentalis* L.	White	Iftner et al. (1992)
Sapotaceae	*Bumelia lanuginosa* (Michx.) Pers.	White	Ajilvsgi (1990)
Saxifragaceae	*Philadelphus coronarius* L.	White	Shields (1985)
Verbenaceae	*Aloysia sp.*	White or pink	Gilbert (1985)
	Lantana sp.	White, yellow, orange, pink, red, or purple	Opler (1998)
	Verbena bonariensis L.	Purple	Floridata (2006)

[a] Kartesz and Kartesz (1980) treat *Bidens alba* var. *radiata* as *B. pilosa* var. *radiata*, but we recognize *B. alba* var. *radiata* because *B. pilosa* is a junior synonym of *B. alba*, according to a recent study in Florida (Wunderlin and Hansen, 2003).

[b]Since "*Solidago* sp." may represent *Solidago canadensis* or any other *Solidago* species, we exclude this taxon from the statistical analyses of this study.

[c]Gable & Baker (1922) listed *Eysenhardtia amophoides* Kunth as a nectar source. According to McVaugh (1987), *Eysenhardtia amophoides* is a junior synonym of *E. polystachya*.

[d]Kartesz and Kartesz (1980) did not include *Rubus fruticosus*, or list this as a synonym for any other plant species. We therefore maintain the record of Bubna (1897).

white, 20 (30.3%) that are yellow or partially yellow, and 14 (21.2%) that are pink or partially pink. Up to nine records may be purple (13.6%), and red and orange flowers combined constitute less than 10% of all flower visitation records.

While it appears that *L. carinenta* favors white and yellow flowers, we were unable to test specifically for preference, as controlled choice experiments were beyond the scope of this project. Experiments on color preference in butterflies have been limited to several

model butterflies, all non-libytheine species - Papilionidae: *Papilio troilus* L. (Swihart 1970) and *Papilio demoleus* L. (Ilse & Vaidya 1956); Nymphalidae: *Agraulis vanillae* (L.), and *Junonia coenia* Hübner (Weiss 1991), and *Heliconius charithonius* (L.) (Swihart & Swihart 1970). Butterflies are also known to learn different colors during nectar foraging, which can influence color preference (Goulson & Cory 1993, Weiss 1995, Weiss & Papaj 2003). Controlled experimental studies on flower coloration that test for preference and learning should be a focus of future studies on libythine biology.

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The Geometrid Moths of Europe...

I have learned that the North American distributor for Apollo Books, which includes The Geometrid Moths of Europe reviewed in 60(3) p. 179, is International Specialized Book Services, 920 NE 58th St., Suite 300, Portland, OR 97213-3786 (800) 944-6190. They are offering this book for the reduced price of $165.50. Those of you who are interested in this book and who live in North America should contact ISBS.

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(New names in **boldface**)

Journal of the Lepidopterists' Society
60(4), 2004, 238-239

EDITORIAL

This issue marks the end of my tenure as editor. It has been a great experience, and while I admit to some relief, I will miss this "labor of love". I will miss it somewhat less, knowing I leave it in the capable hands of my successor, Brian Scholtens, who assumes the role of editor on 1 January 2007. Along the way, a great many people have helped me as I took on this task. Special mention goes to Carla Penz, who spent quite a bit of time breaking me in before she handed over the editorial reins. I hope the transition between myself and Brian goes as smoothly as the transition between Carla and me. Also, I must mention my wife, Peg, who took on the duties of layout editor and whose aesthetic judgement has markedly improved the *Journal*. She's the one who suggested we institute a color cover — after all, we're dealing with some of the most beautiful creatures on Earth! Many of you have served as reviewers, and that sometimes thankless task has been essential to our science. Please know that I am extremely grateful to all of you. Bob Robbins and the Smithsonian provided funds to increase color publication, and we should all be grateful to them.

We are entering a period of transition with regard to Society publications. Right now, we are discussing electronic publishing, which would mean a more timely appearance of articles. We have had feedback that the *Journal* is perceived to be of less importance to many members; some have sensed a resentment that member dues support a publication that isn't read. I don't know whether those perceptions are accurate. I do know that the *Journal* is absolutely essential to this Society.

When I joined the Society in 1963, I couldn't wait for the next issue of the *Journal*. At that age, the idea that there were new species awaiting discovery, perhaps in my own backyard, had tremendous appeal. Articles about "hit and run" collecting trips to my home state, and the genetics of pierids got me more and more excited about my "critters". Of course, the *Journal* has changed from those days, because our science has changed. There are still lots of taxonomy papers, but now the descriptions might well include DNA "bar codes". There are more papers on behavior, ecology, evolution — and few to none of the "hit and run" collecting trips of the past. The sense some have is that the articles that appear in the *Journal* are of little to no interest to the butterfly watchers and recreational lepidopterists among us.

I sincerely hope that is not true. I have "graduated" from collecting to watching, but my watching is not to add another species to my life list. I watch butterflies and moths to learn how they live, and I can learn a great deal watching even the commonest species. What I read in the *Journal* has great relevance for my watching activites — for example, see Dale Schweitzer's excellent papers in this volume on the overwintering patterns of some of our commonest moths and butterflies. I hope all of you will read the articles in the *Journal*, regardless of your particular interests. I guarantee that even articles which seem to have no relevance for what you do as a lepidopterist will make your appreciation for our favorite beasts grow. And the efforts of the researchers who study moths and butterflies and publish their observations in the *Journal* will provide an archive of understanding for future curious lepidopterists, including those 13-year-olds who, like me in 1963, are just begining to recognize the wonder of the natural world.

— Mike Toliver

Date of Issue (Vol. 60, No. 4): 14 December 2006

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

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